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MELBOURNE

ADULT REPRODUCTIVE BEHAVIOUR IN *ASOLCUS BASALIS* (HYMENOPTERA: SCELIONIDAE)

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[Manuscript received July 14, 1961]

Summary

Adult reproductive behaviour in *Asolcus basalis*, a solitary parasite of the egg masses of *Nezara viridula smaragdula*, presents various remarkable features. These include: male aggressive behaviour, in which one male takes possession of an egg mass and drives away all other males; high male mating capacity, which permits the possessing male to fertilize virtually all females emerging from the egg mass it possesses; marking of the host by the female after parasitizing it, this being the basis for a considerable ability on the part of females to discriminate between parasitized and unparasitized hosts; and female aggressive behaviour in which one female drives all other females from an egg mass as soon as it is more or less completely parasitized. It is thought that the value to the species of these and other features of adult behaviour is that they increase the total female searching capacity for hosts. It is suggested that similar forms of reproductive behaviour may be widespread in some groups of the Scelionidae.

I. INTRODUCTION

Asolcus (Microphanurus) basalis (Wollaston) (= *Telenomus megacephalus* Ashmead) is an egg parasite of *Nezara viridula smaragdula* (F.) (Pentatomidae). The adult parasites exhibit patterns of behaviour associated with reproduction which are of unusual interest. The paper describes this behaviour.

II. MATERIAL

The culture of *A. basalis* used was obtained from the Commonwealth Institute of Biological Control and originated in Montserrat, British West Indies. Specimens were identified by C. F. W. Muesebeck, United States Department of Agriculture, and G. E. J. Nixon, Commonwealth Institute of Entomology.

III. GENERAL BIOLOGY

A. basalis is a solitary, arrenotokous parasite, which completes development from egg to adult within the host egg. Eggs killed in a deep-freeze refrigerator form satisfactory laboratory hosts.

A. basalis passes through a number of generations each year. Development is rapid at high temperatures. At 80°F, for example, the developmental period from egg to adult is as shown in Table 1. Adult life is rather brief. In six pairs kept at 80°F, the males lived for 4-5 days and the females for 4-15 days. The number of offspring produced by individual females varied between 104 and 187.

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The females began to oviposit on the day of emergence and, in the presence of ample hosts, deposited practically all their eggs during the first 4 or 5 days.

Information on the biology of this parasite is given by Noble (1937) and Kamal (1938), who found that several eggs sometimes occur in one host. Superfluous individuals are eliminated in the first instar by larval combat.

IV. OVIPOSITION BEHAVIOUR

The egg masses of *Nezara viridula* consist of about 50–90 barrel-shaped eggs adhering compactly in parallel rows. The oviposition behaviour of the female parasite normally operates in response to such an egg mass, but the female will nevertheless readily parasitize single eggs or small groups.

TABLE 1
DEVELOPMENTAL PERIOD IN *A. BASALIS* REARED AT 80°F

Days after Host Parasitized	No. of Adults Emerged	
	Males	Females
9	17	—
10	21	—
11	25	33
12	2	44
13	1	14
14	1	9
15	—	2

When the female encounters an egg mass, she walks over it, and examines the eggs by antennal palpation. The antennae of the female differ from those of the male in being clavate instead of filiform, and the enlarged terminal segments are flattened and slightly curved, and are thus adapted for contact with the convex surfaces of the host egg.

An egg mass consists of inner eggs, which are accessible to the parasite only at their upper surfaces, and eggs on the periphery, which are accessible both at their upper surfaces and exposed sides. When the female examines the upper surface of an inner egg, she palpates the operculum, and often rotates on the egg, exploring with her antennae the crevices between it and adjacent eggs. The examination is usually thorough but completed quite quickly. When the female examines peripheral eggs, the extent of her exploration is variable, and depends partly on whether she first encounters the egg at its side or top. She may examine the whole of the exposed surface, or only the lateral or the upper surface.

The female seldom oviposits through the operculum, which is probably more resistant to penetration. Peripheral eggs are almost always stung laterally, and inner eggs usually just below the chorionic processes. After selecting an egg for oviposition, the female moves to an adjacent egg and, facing away from the intended host, brings the ovipositor into contact with the host at a point usually in or near the crevice between the two eggs. When stinging a peripheral egg, the

female may stand on an adjacent egg or on the substratum. During oviposition, the body is held practically at right angles to the egg surface and there are slight movements of the body and ovipositor.

After the female has oviposited, it withdraws the ovipositor, and raises the body high, the prothoracic legs often being lifted from the egg surface. The female then weaves the ovipositor to and fro across the egg surface, bringing the tip of the ovipositor frequently into contact with the egg as if an exudate were being dabbed on it. The area touched by the ovipositor is usually that which the female can reach as she straddles the egg. This permits the whole operculum of an inner egg to be so treated, or the side or the operculum of a peripheral egg, according to where the ovipositor was inserted.

The female is able by palpation (see below) to distinguish parasitized from unparasitized eggs, and it seems certain that this marking of the parasitized egg is the basis for discrimination. In examining eggs for the selection of hosts for parasitism, the female spends little time in examining an egg which has been marked, and quickly passes on to examine another.

TABLE 2
FREQUENCY OF STINGING OF HOSTS EXPOSED IN SINGLE EGG MASSES
TO ONE FEMALE (SERIES 1) AND TWO FEMALES (SERIES 2) OF
A. BASALIS

Frequency of stinging	Number of Hosts				
	0	1	2	3	4
Series 1	1	66	5	1	2
Series 2	2	57	11	4	1

It happens on rare occasions that a female intending to sting an egg which she has examined, in error stings an adjacent egg, but it is the intended host which seems usually to be subsequently marked. Such errors are caused mainly by irregularities in the alignment of the eggs. It also occasionally happens that a female, disturbed by another while engaged in marking an egg, marks the wrong egg when it resumes marking.

In an experiment carried out at laboratory room temperature, single egg masses gummed to cardboard slips were exposed to fertilized females, 0-2 days old, for parasitism. Each egg mass, cut from a larger one, consisted of 25 eggs in the form of a parallelogram of five rows of five. The experiment consisted of two series, each carried out in triplicate. In series 1, each egg mass was exposed to one female, and in series 2, each was exposed to two females. The activities of the females were recorded during the several hours that they remained interested in their hosts, all or practically all the eggs being stung during the period of observation.

The combined replicates for each of the two series gave the frequencies of stinging among the 75 hosts shown in Table 2.

Altogether, there were 87 stings in series 1 and 95 in series 2. If these were distributed at random* among the hosts, they would give approximately the stinging frequencies shown in Table 3.

TABLE 3
CALCULATED STINGING FREQUENCIES WHEN TOTAL STINGINGS OF HOSTS
BY SINGLE FEMALES (SERIES 1) AND PAIRS OF FEMALES (SERIES 2) OF *A. BASALIS*
ARE DISTRIBUTED RANDOMLY AMONG THE AVAILABLE HOSTS

Frequency of stinging	Number of Hosts				
	0	1	2	3	4 or More
Series 1	23	27	16	6	2
Series 2	21	27	17	7	3

The observed distributions (Table 2) clearly depart significantly from randomness. Combining classes 3 and 4, as the expected number with 4 or more stings is low, the value of χ^2 (with two degrees of freedom) is 86.50 for series 1 and 55.40 for series 2. The observed distributions in series 1 and 2 are similar, and no significant difference between them was shown by the tests applied.

The frequency with which the 75 eggs of each series were marked by the females is shown in Table 4.

TABLE 4
FREQUENCY OF MARKING OF HOSTS EXPOSED IN SINGLE
EGG MASSES TO ONE FEMALE (SERIES 1) AND TWO FEMALES
(SERIES 2) OF *A. BASALIS*

Frequency of marking	Number of Hosts			
	0	1	2	3
Series 1	6	68	1	—
Series 2	5	59	9	2

In series 1, the eggs were seldom stung again after being marked, and seldom marked more than once. Of the six eggs not marked, five were stung (1-4 times) but no parasites developed. It appears, therefore, that no eggs were laid, and it is evident that the marking of the host usually if not always only follows actual egg deposition. The female obviously exercises a choice as to the suitability of the host after insertion of the ovipositor. Peripheral eggs tended to be stung

*If s stings are distributed at random among n hosts, the expected number of hosts to receive r stings is $\{s!/r!(s-r)!\} \cdot (n-1)^{s-r}/n^{s-1}$.

earlier than inner eggs, which is understandable in view of their greater exposed area. Also, as oviposition progressed, the proportion of eggs that were stung but not marked tended to increase, because eggs which had been rejected as hosts necessarily formed an increasing fraction of the unmarked eggs.

In series 2, multiple marking was more common, and much of this arose from concurrent oviposition in the same host by two females, which occurred in six hosts, all of which were peripheral. Of the five eggs not marked, three were stung (1–4 times) but showed no subsequent parasite development, whilst of 70 marked hosts, only two showed no parasite development. Multiple stinging occurred more frequently in the later stages of parasitization of the egg masses as unmarked hosts became less numerous. Multiple marking of the host presumably involved multiple oviposition, but none of the eggs concerned produced more than one adult.

It is evident from this experiment that a female can to a substantial degree avoid depositing eggs in hosts already oviposited in, whether by itself or another female.

The duration of the act of stinging (from beginning of drilling to withdrawal of the ovipositor) was timed for the stings of two females. The duration differed greatly, ranging from about 2 to 15 min, and averaged about 3 min in one female and 6 min in the other. The duration of the act of marking the host after stinging was timed in 16 instances; the mean was 20 sec and the range 14–25 sec.

The time spent by the female in selecting the next host for stinging was usually less than a minute from the time she completed marking the previous host. Selection was sometimes made within 10 sec, but occasionally, particularly as parasitization of the egg mass neared completion, the period of search extended over 1 or even 2 minutes. At the end of parasitization of the egg mass, the female may search for unmarked eggs for 15 or more minutes before abandoning the search.

In series 2, the two females on each egg mass exhibited mutual aggression. One female would rush at the other and drive her temporarily from the egg mass. Such aggression occurred on as many as five occasions in a single replicate. Aggression was shown first by one female and then by the other, and was usually first displayed at an early stage of parasitization of the egg mass. The females then became less sensitive to each other's presence until parasitization was complete or nearly so; then one became highly aggressive, and drove the other permanently from the egg mass. The remaining female continued to search for unmarked eggs for some while, and then also left the egg mass.

Female aggressiveness is seen even more clearly if a larger number of females (say 10) is placed with an unparasitized egg mass. They immediately begin to examine eggs and oviposit. Little aggression is displayed, but occasionally a female leaves the egg mass temporarily as a result of aggression or even of accidental contact with another female. Females which leave the egg mass display some timidity about returning and resuming oviposition. When parasitization of the egg mass is nearly completed, one female suddenly becomes highly aggressive.

This aggressive behaviour is probably elicited by failure to find unmarked hosts. The female dashes about the egg mass, fluttering its wings, attacking the other females in turn, and occasionally biting them. The others do not defend themselves. Those which are merely engaged in searching for hosts retreat from the egg mass; for a while they attempt to return and resume their search for unmarked hosts, but further attacks make them increasingly timid, and they eventually leave the egg mass permanently. Females which are ovipositing endure the attacks passively; the attacker temporarily desists, and ovipositing females are not driven from the egg mass until they have completed the act of oviposition. Driving the females from the egg mass may occupy about 10 min, and it may be another 20 min before attempts to return to the egg mass finally cease. The female left in possession usually searches for unmarked hosts for 15 min or so, and then quits the egg mass herself. If at any stage the aggressive female is removed, her role is assumed by another female.

TABLE 5
PERIODICITY OF ADULT EMERGENCE IN *A. BASALIS*

Day	Time	Number of Adults Emerged			
		Overnight		Day	
		Males	Females	Males	Females
1	10.45 a.m.			1	—
1-2	5 p.m.—8.30 a.m.	2	—		
2-3	5 p.m.—4 a.m.	2	—		
3	4 a.m.—12.20 p.m.			4	—
3-4	5 p.m.—4.30 a.m.	1	1		
4	4.30 a.m.—11 a.m.			1	7
4-5	5 p.m.—4.15 a.m.	2	4		
5	4.15 a.m.—12.05 p.m.			1	17
5-6	5 p.m.—4.30 a.m.	—	6		
6	4.30 a.m.—12.15 p.m.			—	8
Totals		7	11	7	32

V. ADULT EMERGENCE

It is seen from Table 1 that the mean developmental period is shorter for males than females, and that at 80°F only males emerge during the first two days, the proportion of females emerging gradually increasing thereafter. Most males emerge before the first females.

Adults emerge predominantly in the morning. Eggs containing nearly mature parasites were kept in a laboratory room in which the temperature was lowest (66–69°F) about 4 a.m. and highest (75–79°F) about 6 p.m., and adult emergence was recorded for several days and gave the results shown in Table 5. Over two-thirds of the adults emerged during the daytime observational hours. These adults

emerged rather steadily from 4 a.m. until 11 a.m., but only three emerged between 11 a.m. and 1 p.m., and none between 1 p.m. and 5 p.m. Possibly emergence in *A. basalis* is largely restricted to the morning period of rising temperature.

The adult emerges through a round hole cut in the operculum. The time occupied by the operation depends both on temperature and humidity, and usually took about an hour in the laboratory. The adult begins by gnawing at the centre of the operculum until a small hole is produced and one mandible can be exerted; then, with a mandible working on each side, the adult cuts a succession of crescent-shaped pieces until the hole is large enough.

VI. MALE BEHAVIOUR

A male emerging from an egg mass takes possession of it if it is not already possessed by another. The possessing male seldom leaves the egg mass, and its behaviour is affected by the approach of another male. The possessor is then obviously agitated; it patrols the perimeter of the egg mass, standing on the edge facing the approaching male, ready to defend the egg mass against encroachment. The possessing male dashes at the intruder — usually as it is about to mount the egg mass — causing it to retreat. In dashing at the intruder, the possessing male sometimes leaves the egg mass (rarely further than 1 cm), but usually remains on it or retains contact by the hind legs. There is seldom physical contact between the possessor and intruder. The intruder usually makes several attempts to mount the egg mass, but always retreats when attacked, and eventually withdraws entirely.

The aggressiveness of the male depends on possession of the egg mass. If the possessor be removed and the intruder allowed to mount the egg mass, this male then becomes the possessor and displays aggressive dominance over any male, including the former possessor.

The aggressiveness of the possessing male can be fully seen by bringing together two egg masses, each in the possession of a male. The males become aware of one another at a distance of an inch or so, and show increasing aggressive agitation as the egg masses come closer. When the egg masses are contiguous, they form, in effect, a single egg mass with two possessing males. A combat then takes place in which the interlocked males bite severely. The struggle lasts about half a minute, and ends when one male withdraws, usually more or less incapacitated by damage to an antenna or elsewhere.

In the absence of intruding males, the possessing male attends to the egg mass, but the attention given depends on whether adults are attempting to emerge.

The male moves about the egg mass, examining the opercula by palpation. If no emergence activity is taking place, the male becomes inactive, intermittently examining the eggs, but chiefly resting, usually on one of the vertical sides of the egg mass. As there are often lengthy intervals between emergences, especially as emergence tends to be concentrated in the morning hours, there are long periods of inactivity before the females begin to emerge. Under these conditions, the possessing male may move from the egg mass and settle nearby (returning occasionally to examine the eggs), or may even leave the egg mass permanently. For this reason (even ignoring the complication of males from other sources)

it is not necessarily the first male to emerge from an egg mass which is in possession when the females begin to emerge.

For example, in an egg mass observed during the days of the emergence period, it was the third male to emerge which had possession while the females were emerging. Other males on emergence were driven from the egg mass by a possessing male, but the first three males (which emerged during $1\frac{1}{2}$ hours on the first morning of emergence) each took possession at different times when the egg mass was temporarily abandoned. The third male was in possession for 15 min on the first day of emergence, again took possession on the second day, remained in possession for the next 2 days, and then settled some distance from the egg mass, no males being in possession from this time. This male was in possession while all except the last four females emerged. It was observed to mate with many females, and probably did so with all except the last three of the 42 females emerging.

During periods of emergence activity, the possessing male (if not distracted by intruding males) is very active in moving about the egg mass to palpate in succession at each hole being cut by an emerging adult. The male gives particular attention to the larger holes and returns most frequently to the largest. When an adult is on the point of emergence, the male stands over the egg palpating the hole, and mounts the adult as it emerges, palpating its head. If the emerging adult is a female, she lowers her head, and mating occurs immediately, occupying only a few seconds. The mated female leaves the egg mass, and the male resumes examination of the emergence holes.

The possessing male usually reacts initially in the same way to an emerging male. It stands over it during emergence, mounts it, and palpates its head, but when the emerging male fails to respond appropriately, it is driven from the egg mass. Occasionally, a possessing male seems to recognize an adult as a male before it has emerged completely, and its behaviour is modified accordingly.

VII. MALE CAPACITY TO FERTILIZE

The capacity of the male to mate effectively with many females was studied in a male whose mating history was fully known. The male, kept in a laboratory room and provided with honey and water, died on its ninth day. It was provided intermittently with virgin females for mating. Altogether, 72 females were provided, and the male copulated with all. After mating, each female was isolated with an egg mass for 3 days at 80°F and the progeny subsequently reared, and the criterion of effective mating was the occurrence of female progeny. Ten virgin females, provided similarly with egg masses, gave rise only to male progeny (mean 51, range 32 to 62 per female).

The results obtained are given in Table 6. The male effectively mated with 56 of the females, which gave rise to 2004 female progeny. The greatest number of females effectively mated on one day was 16. It may be assumed that temporary sperm depletion was the reason for the ineffective matings. The sex ratio of the progeny was about 1 male : 5 females for the 56 effectively mated females, and about 1 male : 2 females for all 72 females.

VIII. DISCUSSION

The Scelionidae have specialized as parasites of eggs, especially those of Heteroptera and Orthoptera. Scelionids are generally solitary parasites, though some species are gregarious. Frequently, the eggs parasitized are deposited in masses, as in the subterranean egg batches of locusts and grasshoppers, the single-layer egg masses of pentatomids, and the multi-layer egg masses of some Lepidoptera. The scelionids have been very successful in occupying this ecological niche; they constitute one of the most important and numerous families of egg parasites, and, at least as parasites of pentatomids, seem often able to achieve a high percentage parasitism of their hosts. The family is of much interest biocoenotically, and several species have been used effectively in attempts at biological control.

TABLE 6
SEX OF PROGENY OF FEMALES OF *A. BASALIS* MATED WITH THE SAME MALE

Day of Male's Life	Total Females Mated	Females Effectively Mated			Females Not Effectively Mated		
		No. of Females	No. of Progeny		No. of Females	No. of Progeny	
			Males	Females		Males	Females
3	8	8	63	311	—	—	—
4	21	15	108	537	6	235	—
5	15	12	101	485	3	179	—
7	22	16	128	573	6	262	—
8	6	5	15	98	1	45	—
Totals	72	56	415	2004	16	721	—

In recent years, understanding of host selection by parasites, their ability to discriminate between parasitized and unparasitized hosts and to exercise restraint in oviposition, and related matters, has been considerably extended, but the scelionids have received little attention in such studies. This deficiency is important because the kind of reproductive behaviour exhibited by *A. basalis* differs greatly from the general pattern of behaviour customarily found in parasites of other groups. It is desirable, therefore, to consider whether reproductive behaviour similar to that of *A. basalis* may be frequent in scelionids. This is best done by considering in turn the main characteristics described for *A. basalis*.

- (1) *Marking of the host egg after parasitization.* There are a number of observations on female behaviour after withdrawal of the ovipositor from the host which suggest that the marking of the host may be common in scelionids. *Telenomus ashmeadi* Morrill (Morrill 1907) scrapes the host with the ovipositor. *Trissolcus simoni* Mayr. (Voukassovitch 1925) rubs the tip of the ovipositor against the egg. *Telenomus cosmopeplae*

Gahan (Balduf 1926) brushes the host with the still-protruded ovipositor. *Telenomus fariai* Lima (Lima 1928) walks over the egg trailing the ovipositor. *Microphanurus painei* Ferriere (Lever 1933) wipes the ovipositor on the chorionic processes.

- (2) *Female ability to discriminate between parasitized and unparasitized hosts and to exercise restraint in oviposition.* These abilities seem to be common and, though superparasitism occurs, to be generally of a high order; they have been indicated for *Trissolcus simoni*, *Telenomus cosmopeplae*, *Telenomus fariai* (Lima 1928), *Telenomus ullyetti* Nixon (Jones 1937), and *Telenomus gifuensis* Ashmead (Hidaka 1958). According to McColloch (1915), *Eumicrosoma benefica* Gahan is unable to discriminate, but this needs confirmation. Simultaneous oviposition by more than one female in the same host has been recorded in *Microphanurus painei*, *Telenomus nawai* Ashmead (Pemberton 1933), *A. basalis* (Noble 1937; Kamal 1938), and *Microphanurus* sp. (Chatterji and Rahalkar 1958).
- (3) *Aggressiveness of the ovipositing female.* Fighting or aggressiveness in females has been reported from *Trissolcus simoni*, *Telenomus cosmopeplae*, *Telenomus gifuensis*, and *Microphanurus painei*.
- (4) *Diurnal periodicity of adult emergence and emergence of males before females.* Indications of an emergence periodicity have been found in *Eumicrosoma benefica* (McColloch and Yuasa 1914) and *Telenomus gifuensis*. Earlier emergence of the males is recorded in *Telenomus nawai*, *Telenomus gifuensis*, and *Microphanurus semistriatus* Nees (Zomorodi 1959).
- (5) *Male aggression leading to possession of an egg mass by one male.* Combat between two males emerging at the same time has been reported in *Telenomus gifuensis*.
- (6) *Immediate fertilization of each female on emergence.* Insemination of females on emergence, or the ability to mate on or soon after emergence, has been indicated in *Telenomus nawai*, *Telenomus ullyetti*, *Telenomus fariai*, *Telenomus gifuensis*, and *Hadronotus ajax* Girault (Schell 1943).
- (7) *High mating capacity of the male; the fertilization of nearly all females by one male.* A high mating capacity has been indicated for males of *Eumicrosoma benefica* (McColloch 1915), *Telenomus ullyetti*, and *Telenomus fariai* (Dreyfus and Breuer 1944), though the stated capacity is low by comparison with *A. basalis*. In *Telenomus fariai*, a gregarious parasite, mating takes place before the adults issue from the host, and one male can fertilize all the females present.
- (8) *Numerical preponderance of females.* In the Scelionidae, females seem generally to be more numerous than males. Male : female ratios recorded are *Telenomus ashmeadi* 1 : 5.7, *Hadronotus ajax* 1 : 5, *Telenomus fariai* 1 : 5, *Eumicrosoma benefica* 1 : 3, *Telenomus ullyetti* 1 : 2.5, and *Telenomus nawai* 1 : 1.3.

This summary suggests that some of the characteristics of reproductive behaviour in *A. basalis* are found in somewhat similar form in other scelionids, and that the family, or groups within it, have developed some forms of behaviour which are markedly different from those of most other hymenopterous parasites.

Two other scelionid behavioural records of interest are those of male assistance to a female unable to release its ovipositor (reported from *Telenomus nigrocoxalis* Ashmead by Squire (1932)), and the occurrence of phoresy in *Phanurus beneficiens* (Zehnt.), the adults of which are transported on the bodies of a pyralid moth (van Vuuren 1935). Phoresy is also known to be employed as a means of reaching host eggs by scelionid parasites of Orthoptera (Clausen 1940).

The question arises as to the value to the species of the reproductive behaviour found in *A. basalis*. The general results of this behaviour seem to be the following: Female discrimination and restraint in oviposition tend to ensure complete parasitization of an egg mass, and to reduce superparasitism. Female aggression reduces the time wasted in searching parasitized egg masses, and increases the time spent in searching for unparasitized egg masses. Male aggression and capacity to mate tend to ensure that females are mated as they emerge, and to increase the number of males available in the general environment (as distinct from the egg masses yielding adults) for the fertilization of females that are unmated or willing to mate again. As mated females tend to produce a high proportion of female progeny, male aggression and capacity to mate tend to increase total female searching capacity for hosts.

The behaviour described has seemingly developed in relation to hosts which occur in aggregates and are generally available for parasitism for a comparatively short period. The main advantage provided by the behaviour appears to be an increase in female host-searching ability, and this may be basic to the considerable success achieved by some scelionids in the ecological niche they occupy.

In nature, there is undoubtedly a tendency for an egg mass to be parasitized entirely by a single female of *A. basalis*, for all females emerging from an egg mass to be fertilized by one male, and for this male to be the brother of the females it mates. Brother-sister matings must be common and possibly the rule, but non-brother-sister matings are probably not infrequent.

In *T. fariai* (Dreyfus and Breuer 1944) brother-sister matings are said to be usual if not invariable. In this species the male has 10 chromosomes and the female 20. It is reported that X- and Y-chromosomes occur in the females and that there is an unequal division in the spermatogonia, but White (1954) finds the evidence unconvincing. Dreyfus and Breuer suggest that there may be a connection between the unusual chromosome behaviour they describe and the occurrence of brother-sister mating, but they do not indicate what this connection might be. As brother-sister matings are probably very common in many scelionids, and as their occurrence and usefulness can apparently be adequately explained in another way, there seems to be no sufficient reason for postulating a cytological explanation. It seems that the frequency of brother-sister mating is incidental to a pattern of behaviour which has evolved in relation to the occurrence of hosts in aggregates, and that it is this host characteristic which gives the behaviour relevance and makes it of value to the parasite.

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THE USE OF SAMPLING METHODS IN STUDIES OF THE DISTRIBUTION OF LARVAE OF *BOOPHILUS MICROPLUS* ON PASTURES

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Summary

Three methods of sampling pasture for larvae of *Boophilus microplus* (Can.) were tested by traversing plots which had been artificially infested with known numbers of larvae. A wheeled device gave the highest yield, picking up about 5% of larvae encountered, as against 2.5-3% for white cloth leggings and 0.5% for a cotton blanket 18 in. wide.

In a later test in naturally infested pasture there was no significant difference between numbers of larvae picked up by a modified form of a sampling device described by Blagoveschenskii (1957) and the wheeled sampler. However, Blagoveschenskii's sampler was easier to use than the wheeled sampler. The leggings can be used in rough or heavily timbered country which is unsuitable for the other sampling devices.

Further tests indicated that a suitable length for sampling transects is 50 yd, and that it was advantageous to carry out both "forward" and "return" traverses on each transect. There was no evidence of difference in yield between early morning and noon traverses.

Legging samplers, supplemented by blanket dragging, were used to obtain information on the relation of larval infestation to cattle habits in an 80-acre paddock, and to compare infestations on a "creek-bank" and a "hillside" plot, in a 400-acre paddock. It was concluded that:

(1) Larvae were widespread in the pasture and at times abundant even in dry grass on dry soil.

(2) Cattle "camps" may be only lightly infested despite the high number of diurnal "cattle-hours" spent there, and possible reasons for this are discussed.

(3) Cattle do not rest in a fixed locality at night but appear to prefer well-drained areas of pasture, which may become heavily infested.

(4) The grazing habits of cattle, as indicated by dung pat counts, varied with the season in the 400-acre paddock. In the drought of late 1951 heavy grazing of the creek frontage coincided with heavy larval infestation of the creek bank plot.

(5) The wide distribution of larvae reduces the economic feasibility of controlling tick infestations by treatment of pastures with acaricides, particularly where the number of cattle per square mile is low.

I. INTRODUCTION

Pasture sampling methods have provided useful information on the seasonal abundance of the host-seeking stages of ticks, and on their spatial distribution in relation to host habits, vegetation, and other features of the environment, but the literature deals more with three-host ticks than with one-host genera such as

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Boophilus. For *Boophilus*, in addition to these requirements, there is a need for convenient methods of estimating numerical changes in pasture populations following control measures, for example after removing cattle from a paddock (Wilkinson 1957) or after treating either cattle or pastures with acaricides.

The engorged and ovipositing female, the egg, and the larva are the only stages of one-host ticks normally found in pasture. Of these, the host-seeking larvae are the most convenient for sampling, since the other stages are concealed beneath vegetation or soil.

Under natural conditions the female tick moves only a short distance from the point of dropping, and larval groups are usually less than 6 ft from the oviposition site (Wilkinson 1953, 1957). Consequently the distribution of larvae in a paddock will depend chiefly on the distribution of the female ticks, which depends in turn on whether the rate of dropping from the host is random or otherwise, and whether the host covers its territory in a random or a selective manner. There are several references to *Boophilus* and other Ixodidae dropping from the host in a non-random manner with respect to time (Symons 1909; Milne 1950a; Balashov 1954; Hitchcock 1955a), and although some of these refer to stalled cattle, they strongly suggest that the field drop is unlikely to be uniform, or random. Host habits have been reported to influence tick distribution, for instance, *Dermacentor andersoni* is concentrated along game trails (Gregson 1956), and *Otobius megnini* around salt troughs in Texas (Parish 1949). Bonsma (1944) believed that "rank vegetation under trees where cattle rest" was especially heavily infested with ticks. Milne considered that *Ixodes ricinus* L. females dropped at random from sheep (Milne 1950a, 1950b), or showed a "slight tendency" to random spatial distribution (Milne 1943) but elsewhere he stated (Milne 1950a) that probably more ticks drop off during the night, owing to "increased friction aiding the process of detachment".

There have been several studies of cattle behaviour (Cory 1927; Castle, Foot, and Halley 1950; Findlay 1950; Payne, Laing, and Raivoka 1951; Bonsma and Le Roux 1953; Larkin 1954) but few of these refer to beef cattle on unimproved tropical pastures, and there is little information relevant to the study of tick distribution.

In the present paper several pasture sampling methods are compared. In addition, studies of the distribution of larvae in relation to cattle habits, and of the seasonal distribution of larvae on a creek bank and hillside plot, are described.

II. SAMPLING METHODS

(a) *Methods Used by other Workers*

Philip (1937) sampled the population of unfed adult *Dermacentor andersoni* on a 40-acre tract by dragging a yard square "flag" in a zigzag path along five fixed transects. Each transect appears to have been 220 yd long and ticks were released "as soon as caught". The counts for each sampling day were used to illustrate the seasonal trend, over six years.

Milne (1943), working on *Ixodes ricinus* in northern England, trailed a woollen blanket (presumably 70 in. wide) over moorland vegetation, and preferred to sample nymphs, rather than adults or larvae. He used transects 50 yd long, moving to "virgin" strips on each occasion. He found that the distribution of counts was positively skewed and resembled Neyman's "contagious" distribution, but that the ordinary analysis of variance could be used in comparing areas. A numerical example showed that comparison of tick populations is best made by a small number of drags on many days, rather than by a large number on few days. He noted that blankets rode over the taller plants, missing intervening shorter vegetation.

Blakeslee and Bruce (1948) used a piece of white outing flannel to collect larvae of *Boophilus annulatus* (Say) in observations which continued for a short time after aerial spraying.

Snowball (personal communication; see also C.S.I.R.O. Aust. 1950) tested several different devices for sampling *Boophilus* larvae in the Brisbane area. Using a 36-in. wide cotton blanket he found the yield of larvae was low, even when numerous larvae were present, and larvae became embedded in the material and difficult to dislodge. With flag samplers the objection of Milne (1943) held, in that "pace, sweep length, and weight of application of the flag cannot be controlled accurately, while walking over rough ground".

Blagoveschenskii (1957) described a device consisting of a cloth-covered square piece of plywood (side 50 cm) with a handle placed at about 45° to the base of the square. It differs from flag samplers in that it is rigid; the cloth-covered board is held vertically as far as possible, with the lower edge making contact with short grass, or following the contours of the thicker parts of tussocks and obstructions.

The Campbell static blanket method (Heath 1951), and conical metal traps 18 in. in diameter (similar to the paper traps used by Jones (1950) for mites) were tested briefly against the wheeled sampler described below, and yielded only about a tenth of the number of larvae for a similar expenditure of time. The Campbell method would be impracticable in the wet season owing to wet soil, and the conical traps had to be put out the previous night and removed in the early morning, to avoid heating by the sun.

Improvements on these two methods might have the advantage of indicating the locality of larvae more precisely than traversing methods, but an excessively large number of sites might have to be sampled to record light infestations.

(b) Description of Apparatus and Methods Tested in Present Work

(i) *Sampling Devices*.—It was found that blanket dragging had several disadvantages in addition to those mentioned previously. The blanket caught in fallen timber and other obstructions, picked up large numbers of grass and burr seeds, was difficult to control in wind, and rubbed any attached larvae heavily against the vegetation. Moreover the operator picked up many larvae.

It became apparent that a sampling device with a vertical collecting surface, held in front or to one side of the operator, would overcome many of these difficulties. It was also found that a type of trouser legging overcame or reduced many of the difficulties of sampling in rough country (later the use of leggings to test tick repellents came to notice; see Granett and French (1950)). White cotton duck leggings were used, made narrow around the knee and ankle, so that few folds were formed. In use the lower edges were 4–5 in. above ground level. Larvae commonly attached about 18 in. above ground level and were readily found and removed. When the grass became short because of heavy grazing, counts on the leggings were supplemented by blanket counts.

Later, a wheeled sampler was constructed. This retained the sampling surface in a near vertical plane, and made contact with both short and long grass (Plate 1, Fig. 1). The sampling surface consisted of seven 3-in. wide wooden slats, covered with flannelette and hinged to a crossbar. Overall width across the slats was 23 in. and the crossbar was 30 in. above ground level when in use. The cloth covers could be zipped off for cleaning and storage.

The sampler described by Blagoveschenskii (1957) was also tested, and a modified form adopted. A hinge was included between the handle and the flannelette-covered plywood (Plate 1, Fig. 2). With the hinge the handle could be maintained at an almost constant angle relative to the ground surface, since the board was deflected as necessary to conform to the contours of the tussock or other objects encountered. To simplify comparisons with the wheeled sampler, the base of the board was 21 in. wide, equal to the sum of the widths of the barrow slats. This device was termed the “hinged flag” sampler.

(ii) *Marking of Transects and Traversing Procedure.*—The transects to be sampled were marked with gravel-filled 4-gal oil drums, or readily movable steel pickets as used in electric fences. Cattle rarely displaced either of these, and both could be moved to mark the next transect, so the difficulties mentioned by Milne (1943) were not experienced. The transects, 50 yd long, were traversed in about $1\frac{1}{2}$ min. The number of larvae and time taken were noted. The larvae were then brushed off, away from the area, and a return to the point or origin was made in the same way, after which larvae were again counted. In some tests, using the “hinged flag” with removable cloths, the cloths were placed in tins secured to the electric fence pickets (Plate 1, Fig. 2), and were later examined in the laboratory, the larvae being removed by suction pump.

(c) *Details of Tests of Sampling Methods*

(i) *Tests on Artificially Infested Plots.*—The efficiency of the wheeled, legging, and blanket samplers was compared by recording the numbers of larvae picked up from plots of known infestation.

Fifty egg masses were divided into quarters and then put into 200 2 by $\frac{1}{2}$ in. glass tubes, which were incubated at 30°C and high humidity, until after hatching. Ten eggs were removed from each egg mass before quartering, and the aggregate of these tens was weighed. Each quarter egg mass was also weighed individually,

so that the number of eggs in each tube could be calculated. The mean number of eggs per tube was 733, with standard error 196.

A separate series of 15 tubes was kept to observe percentage hatch, by counting emerged larvae and unhatched eggs. Percentage hatch was estimated at 98%.

The test area, near Rockhampton, was known to be free of cattle tick larvae, since it was unstocked and burnt annually. About half the area was covered with grass 1–3 ft high, with a few weeds up to 3½ ft, the remainder consisted mainly of grass 2½–6 in. high.

On May 31, 1954, two plots each 30 by 50 yd were seeded with larvae by distributing the opened tubes along transects at right angles to the sampling transects. There were ten of these "seeding transects", each 5 yd apart. On plot 1 five tubes of larvae were placed along each transect, at the rate of one tube to every 6 yd. Within each 6-yd space, the tube was placed centrally within a 1-yd space selected by reference to random sequences of numbers 1 to 6.

On plot 2, 15 tubes were distributed on each transect in a similar manner, but one tube to every 6 ft. Thus there were approximately 35,920 larvae on plot 1 and three times this number on plot 2.

Plot 1 was sampled first (Table 1). The wheeled sampler was used by one observer and the other walked alongside wearing the leggings and towing the blanket. The sampling devices were then used on a return trip on the same transect. Eighteen traverses, each 50 yd long, were made, the first two spaced at 4-ft centres, and the remainder at 6-ft centres. Sampling commenced at 8.30 a.m. (local time) and ended about 10.00 a.m.

Plot 2 was sampled with 15 traverses at 6 ft spacing. Times of sampling were arranged to test whether early morning, noon, or evening sampling would yield the most larvae (Wilkinson 1953).

From the results (Table 1), the ratio of larvae picked up (sum of forward and return traverse) to larvae in the path of the sampler can be calculated. The number of larvae encountered is derived from the expression:

$$\frac{\text{No. of larvae put out} \times \text{No. of sampling transects} \times \text{Sampler width}}{\text{Width of area}}$$

Effective swath widths of the samplers were: wheeled 21 in., blanket 18 in., leggings approximately 12 in. (6 in. per leg). On this basis the ratios of larvae picked up : larvae encountered were wheeled 1 : 19 (660/12,572), legging 1 : 44, and blanket 1 : 245. The proportions picked up may have been greater since many larvae may die on grass in the first week of exposure (Wilkinson and Wilson 1959).

On plot 2 the ratios were wheeled 1 : 22, legging 1 : 28.6, and blanket 1 : 201, if the assumption is made that the number of larvae had fallen to twice the number of plot 1 rather than three times as originally seeded, due to natural mortality.

An analysis of variance (using a $\sin p' \sqrt{x}$ transformation) showed a strong interaction between catches on the three types of samplers and time of day, but

no explanation for this observation is available as yet. A similar comment applies to the difference in ratio of larvae picked up on forward and return traverses, on the two plots. The wheeled sampler return catch is much less than the forward catch on plot 1 ($P < 0.001$ using the sign test, 18 positives, no negatives) and the trend is the same for the other samplers. On plot 2 the return traverse picked up nearly as many larvae as the forward traverse, for all samplers, and the difference could be accounted for by the numbers removed.

These complications were avoided in estimating the significance of differences in catches by calculating catch per foot width of the sampling device, on forward traverses only; results are shown at the foot of Table 1.

There was no significant effect of time of day on yield of larvae. Meteorological conditions during sampling of plot 2 are summarized in Table 2.

TABLE 2
METEOROLOGICAL CONDITIONS RECORDED IMMEDIATELY FOLLOWING TESTS OF SAMPLING DEVICES
ON PLOT 2, REFERRED TO IN TABLE 1
Readings on whirling psychrometer

Conditions	7.vi.54			11.vi.54			15.vi.54		
	a.m.	noon	p.m.	a.m.	noon	p.m.	a.m.	noon	p.m.
Shade temp. (°F)									
Dry bulb	60	70	62	63	67	62.5	68	78	73
Wet bulb	—	55	53	51.5	53	51.5	62.5	63	65
Sun*	O	U	O	U	U	U	U	U	U

* O, obscured; U, unobscured.

(ii) *Comparison of Wheeled and "Hinged Flag" Samplers.*—The efficiency of the samplers was compared in a 35-acre paddock occupied by five infested cattle, at Amberley Field Station in southern Queensland. Within the rectangular paddock, six adjacent rectangular areas, each measuring 360 yd by 50 yd, were pegged out, leaving room for access lanes. The six areas occupied about 65% of the paddock, the remainder being too rough or otherwise unsuitable for sampling.

This arrangement allowed 540 possible transects, each 50 yd long and 4 yd apart. Of these, 240 were selected at random, to allow for 10 transects being covered by each method on each of 12 sampling days. Sampling with both devices began simultaneously, at approximately 4 hours after sunrise. To avoid bias towards starting always in the same region, and to reduce the large amount of walking between transects, the area was stratified down the long axis, and the stratum and transect in which to start were determined by random numbers. Sampling was carried out in this manner on 11 occasions between October 1958 and February 1959 (Table 3). There was no significant difference in catch between the two methods. Counts of ticks on the cattle in the paddock are also

shown. The cattle counts show significant positive correlations with the pasture counts, indicating that adequately large areas were sampled on both pastures and cattle, and that the cattle and mechanical devices were sampling the same population.

TABLE 3
COMPARISON OF COUNTS ON TWO PASTURE SAMPLING DEVICES, WITH COUNTS ON CATTLE

Date of Sampling	Pasture Sampling		Cattle Counts (interval from pasture sampling shown in brackets*)		
	A	B	C	D	E
	Larvae Taken on Wheeled Sampler	Larvae on Modified Blagoveschenskii Sampler	Larvae on One Flank and One Dewlap Area† (totals from 5 animals)	Adult Ticks 0.5 cm Length, on Right Sides of Cattle (mean of 5 animals)	Counts as in Column D but Longer Intervals
20.x.58	312	175	—	—	—
24.x.58	226	300	130 (−1)	16.0 (+13)	18.2 (+20)
7.xi.58	256	241	103 (−1)	34.6 (+13)	34.4 (+20)
14.xi.58	438	Not used	104 (−1)	34.4 (+13)	25.2 (+21)
21.xi.58	247	303	90 (−1)	25.2 (+13)	—
28.xi.58	396	212	40 (−1)	—	10.8 (+21)
5.xii.58	11	35	15 (−1)	10.8 (+13)	9.0 (+18)
17.xii.58	20	94	29 (+1)	8.8 (+14)	16.0 (+22)
9.i.59	51	30	11 (−1)	12.8 (+13)	13.6 (+20)
30.i.59	12	18	10 (−1)	—	—
3.ii.59	53	4	—	—	36 (+23)
6.ii.59	22	14	24 (−1)	—	—

Analysis of Results

Difference between A and B	Not significant	$t = 0.661$, 10 d.f.
Correlation of A+B with C	Significant ($P = 0.01$)	$r = 0.765$, 8 d.f.
Correlation of A+B with D	Significant ($P < 0.05$)	$r = 0.821$, 5 d.f.
Correlation of A+B with E	Not significant	$r = 0.171$, 6 d.f.

* +, days later; —, days earlier.

† Demarcated by metal ring, internal diameter 2 in.

(iii) *A Further Test on Effect of Time of Day on Yield of Larvae.*—The wheeled sampler was used in a similar manner to that described in the preceding section, to sample two sets of three areas, each set occupying most of a 17½-acre paddock. The work was undertaken primarily to obtain information (to be published elsewhere) on the decline in larval numbers, but it was so arranged that a sampling of 10 transects commenced 2 hours after sunrise (dew prevented

earlier starts), and sampling of a further 10 transects began at noon. The effects of time of day on catch are set out in Table 4.

No significant differences were detected between "early morning" and "noon" catches on either all days or "summer" days, i.e. when maximum shade temperature

TABLE 4
COMPARISON OF LARVAL CATCHES ON WHEELED SAMPLER AT DIFFERENT TIMES OF DAY

Date	Early Morning		Noon		Screen Temperatures for the Day	
	No. of Larvae	Time of Start (a.m.)	No. of Larvae	Time of Start (p.m.)	Max.	Min.
8.ii.57	111	7.15	36	12.05	89.0	72.3
15.iii.57	0	8.05	1	12.00	86.6	68.0
29.iii.57	0	8.03	0	12.02	80.1	59.3
12.iv.57	349	8.05	506	12.00	85.8	68.0
26.iv.57	2878	8.10	456	12.00	86.1	66.0
10.v.57	384	8.20	1989	12.00	80.6	47.8
24.v.57	219	8.26	106	12.00	73.7	34.0
7.vi.57	1003	8.33	2291	12.05	70.8	55.0
24.vi.57	708	8.50	449	12.02	75.6	46.0
5.vii.57	503	8.40	1145	12.05	71.6	35.0
19.vii.57	311	9.25	584	12.02	72.0	42.2
1.viii.57	182	8.30	125	12.00	74.6	38.8
23.viii.57	260	8.35	852	12.03	79.3	51.4
20.viii.57	762	8.30	82	12.03	73.2	43.2
11.ix.57	26	8.00	32	12.05	75.2	49.1
20.xii.57	2	6.55	41	12.00	95.2	63.4
3.i.58	0	7.00	0	12.00	83.5	63.1
8.i.58	9	7.00	0	12.00	82.3	69.4
24.ii.58	215	7.15	43	12.00	90.2	68.6
7.ii.58	398	7.25	227	12.03	88.0	69.6
24.ii.58	750	7.35	587	12.00	84.3	70.0
7.iii.58	160	8.10	840	12.05	87.8	66.6
21.iii.58	44	8.10	27	12.00	84.0	64.3
9.iv.58	0	8.55	0	12.00	80.8	63.8
18.iv.58	0	8.10	7	12.00	79.0	62.8
2.v.58	0	8.45	0	12.01	77.0	55.6

exceeded 80°F, or other days with lesser maximum temperatures. Since strong light rather than temperature might induce concealment of larvae (Wilkinson 1953), the data in Table 5 were extracted from Table 4, to show catches for forward and return traverses on days when the maximum temperature exceeded 80°F and the sun was unobscured at noon. It might be expected, if larvae are concealed at noon, that forward traverses at noon would catch less larvae than forward traverses in the early morning. Alternatively, relatively more larvae might

be caught on return compared to forward traverses at noon, than in the morning, due to the alerting effect of forward traverses bringing larvae out of concealment at noon. None of these differences proved to be significant, so that there is no evidence of effect of time of day on catch in south Queensland.

TABLE 5

COMPARISON OF EARLY MORNING AND NOON CATCHES ON THE WHEELED SAMPLER
Results are for days on which the maximum temperature exceeded 80°F and the sun was unobscured at noon. Data extracted from the original data summarized in Table 4

Date	Early Morning Sampling		Noon Sampling	
	Forward Traverse	Return Traverse	Forward Traverse	Return Traverse
8.ii.57	56	55	16	20
26.iv.57	1425	1453	252	204
10.v.57	220	164	1647	342
20.xii.57	1	1	3	38
7.ii.58	163	235	58	169
24.ii.58	93	657	74	513
7.iii.58	54	106	423	417
Total	2012	2671	2473	1703

(iv) *Availability of Larvae at Night.*—Cattle graze and travel at night, so it was desirable to know whether larvae could be picked up then. Larvae were liberated on two grass plants, and the plants were swept during the next two days

TABLE 6

NUMBERS OF LARVAE PICKED UP IN DAYLIGHT AND AT NIGHT-TIME
S, shadow; M, moonlight

Method	First Day 10.15 a.m.	First Day 10.10 p.m.	Second Day 10.00 p.m.	Third Day 7.30 a.m.
Forearm sweep				
Plant A	10	16 S	60 M	1
Plant B	46	130 M	30 M	0
Cloth sweep				
Plant A	43	96 S	300 M	60
Plant B	18	120 M	26 M	6
Total	117	362	416	67

and night using first the back of the forearm, and then a small cloth flag. The results (Table 6) indicated that at least as many larvae could be picked up at night as in day time.

(v) *Tests of Retention of Larvae on Different Cloths, with and without Cattle Odour.*—The tick infestation of different areas can be compared by simultaneous traversing with any device, as long as the same procedure is used on both areas. However, the higher the catch of larvae, the easier the comparison of lightly infested areas, since fewer traverses will be needed to obtain significant differences. Low catches will result if larvae tend to be readily lost from the cloth

TABLE 7
RETENTION OF LARVAE BY DIFFERENT TYPES OF CLOTH, BEFORE AND AFTER VIGOROUS BRUSHING OF THE CLOTH THROUGH GRASS ABOUT 18 IN. HIGH
Number of larvae before brushing followed by number of larvae after brushing, in brackets

Duck	Impregnated Duck	Flannelette	Impregnated Flannelette
Series A			
4 (1)	8 (6)	24 (18)	9 (8)
45 (9)	28 (23)	15 (11)	14 (11)
11 (7)	16 (12)	22 (6)	10 (10)
9 (6)	36 (27)	20 (6)	32 (17)
45 (18)	17 (9)	8 (5)	14 (14)
15 (7)	22 (8)	9 (5)	17 (10)
8 (4)	25 (9)	9 (7)	12 (4)
3 (1)	15 (13)	6 (6)	26 (23)
46 (17)	8 (8)	18 (9)	5 (3)
14 (14)	21 (11)	14 (5)	10 (6)
200 (84)	196 (126)	145 (78)	149 (106)
Series B			
105 (15)	47 (12)	67 (20)	42 (21)
8 (4)	11 (2)	17 (5)	25 (20)
26 (4)	11 (6)	14 (5)	27 (17)
13 (1)	7 (3)	7 (1)	19 (12)
40 (9)	27 (6)	13 (5)	13 (10)
14 (4)	9 (2)	45 (14)	20 (11)
10 (3)	13 (1)	12 (5)	26 (11)
5 (0)	7 (4)	5 (0)	13 (11)
9 (2)	9 (7)	7 (3)	7 (4)
230 (42)	141 (43)	187 (58)	192 (117)

surfaces, either by falling off or being dislodged by rubbing. Comparisons were made of the retention of larvae by flannelette, as used on the wheeled and hinged flag samplers, and duck cloth, as in the legging samplers. Cattle tick larvae respond to bovine odour (Wilkinson 1953) so further samples of the same cloths were tested after being rubbed over an infested beast.

The cloth samples, 6 in. square, were secured by one edge to wooden handles. These flags were gently trailed over a plant carrying active larvae, and the number of larvae picked up was noted. Each flag was then swept 10 times through uninfested grass about 18 in. high and the number of remaining larvae recorded. Further tests were carried out with the different types of cloth wrapped at intervals round a piece of dowel rod 3 ft long. After catching larvae the rod was dragged over 50 yd of uninfested grass, and the remaining larvae counted.

Table 7 shows retention of the larvae in the two series of tests. The results from the two series were pooled because it was found that there was no significant difference in treatment response. The means for percentage retention (angular transformation) were: impregnated flannelette, 54.70; flannelette 40.95; impreg-

TABLE 8
NUMBERS OF LARVAE PICKED UP ON SAMPLER LEGGINGS, NUMBERS REMAINING
(IN BRACKETS) AFTER WALKING VARIOUS DISTANCES, AND APPROXIMATE
TIMES TAKEN FOR TRAVERSES

Date of Test	12½ yd 25 sec	25 yd 45 sec	50 yd 1 min 25 sec
8.ii.52	43 (15) 27 (4)	5 (1) 4 (0)	8 (0)
12.ii.52	14 (4) 10 (5) 14 (3) 39 (19)	14 (4) 9 (2) 28 (14)	52 (11) 13 (2) 10 (4) 39 (16)
11.iii.52	16 (8) 8 (4)	20 (0) 12 (2)	16 (5) 4 (0)
Percentage remaining	36	25	27

nated duck, 41.45; duck, 34.40. The minimum differences for significance was 7.6 at the 5% level and 10.3 at the 1% level. Effect of both odour and materials was significant at $P < 0.001$, with interaction not significant. The effects were additive for transformed data.

(vi) *Proportion of Larvae Falling from the Leggings during Traverses.*—Some observations were made on this subject, to check the suitability of the length of traverse used.

Larvae were picked up from a marked grass plant which had been artificially infested some days previously. The larvae on the leggings were then counted, before and after walking different distances. It was found (Table 8) that there was no significant difference between the percentage dropping off over the three distances, and the results indicate that 60–80% of the larvae drop off almost immediately after collection, after which the rate of dropping is slow. Consequently

it appears that any length of transect between $12\frac{1}{2}$ and 50 yd can be used for comparing larval infestation of different areas of pasture, provided of course that the same length is used for each area. Lengths greater than 50 yd may prove useful for work with sparse tick infestations, but further tests would be necessary before adopting longer transects.

The practice of carrying out a return traverse as well as a forward traverse on each transect, is doubly justified, since if only one traverse is made larvae picked up near the end will be over-represented in the count, compared with larvae picked up near the beginning of the traverse. Also each transect is more thoroughly sampled than by a single traverse, with little extra effort.

The observations recorded in Table 9 show that appreciable loss of larvae may occur during the delay involved in counting heavier infestations on the leggings.

TABLE 9
NUMBER OF LARVAE REMAINING ON THE LEGGING SAMPLER FOR VARIOUS PERIODS AFTER PICK UP, WHEN THE USER WAS STANDING STILL
Counts of selected groups

Trial No.	No. of Larvae Picked Up	Number of Larvae Present after:					
		10 sec	20 sec	40 sec	80 sec	160 sec	320 sec
1	Not recorded	16	16	15	11	11	9
2	Not recorded	7	7	6	6	6	
3	30		18	13	10	6	
4	13		11	6	4	4	

III. SOME APPLICATIONS OF PASTURE SAMPLING FOR LARVAE

(a) *Larval Distribution in Relation to Cattle Habits*

(i) *Methods.*—The habits and movements of cattle in an 80-acre paddock were studied and, on the basis of this information, larval sampling was carried out in certain defined areas, which were frequented by the cattle during different phases of their activity. Figure 1, and an aerial photograph (Plate 1, Fig. 3) show the vegetation and other major features of the paddock, which was especially leased for the investigation. In March 1952, six spayed cows were admitted to the hitherto empty paddock and three steers were added in June. The animals received no acaricidal treatment; information on their tick infestations has already been published (Wilkinson 1955).

The habits of the cattle, during 24-hour periods commencing at 11.00 a.m., were observed once each month during April to November 1952, inclusive, and in February 1953. To facilitate observations, selected trees and fence posts were marked with paint, and one animal was fitted with a cow-bell. Two observers

took alternate 4-hour watches to plot the movements of the cattle by following them at a distance without disturbing the animals. Binoculars and a spotlight were carried, the latter being used as little as possible. Fortunately the cattle only concealed themselves in the brigalow during the October observations. Most of the nights selected were near the period of full moon, so that the location of the herd could be easily determined, though individual animals lying in long grass were hard to see. The following records were made, at half-hourly intervals:

- (1) Number of minutes spent by the belled animal in the different squares shown on the map (Fig. 2) during the previous 30 min.
- (2) Coordinates (e.g. A1, B3) of all squares occupied at the time, to give extent of spread of animals.

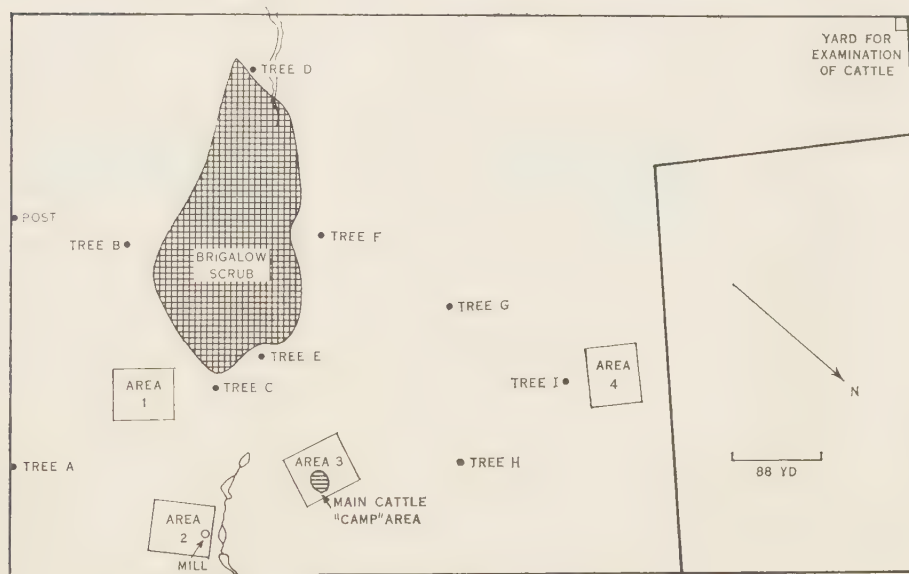


Fig. 1.—Map of 80-acre paddock.

- (3) Proportion of visible animals grazing or walking, as opposed to lying or standing.
- (4) Number of minutes spent by the belled animal in these activities during the previous half hour, and whether this animal was in the shade or open at the time of observation.

The selection of areas for sampling tick larvae was based on the information obtained on cattle habits, up to and including October 1952. Figure 2 shows the total time spent by the belled animal in each square during these observations. The other cattle habitually accompanied the belled animal, being rarely scattered over as much as three squares and often (especially in the "day camp") distributed within a circle of 40 yd diameter.

Areas 1 and 4 were two grazing areas. The first was on flat timbered country, wholly or partly waterlogged in wet weather (e.g. on January 28, February 28,

and March 4, 1953), and was well covered with grass, mostly *Bothriochloa* spp. Area 4 was on treeless, sloping ground and was the most heavily grassed of all areas, the main species being *Heteropogon contortus* (L.) Beauv. ex Roem. & Schult. Area 2 was flat with similar vegetation to area 1, but was less liable to waterlogging; it surrounded the water trough. Area 3 contained the day camp (Plate 3, Fig. 1) which was in a small clump of brigalow. Grass was sparse or absent over most of this area.

	1	2	3	4	5	6	7	8	9	10
F	60	45	120	85	376	170	40	245	20	53
E	55	80	25	510	31	46	457			
D	93	90	10	25	20	310	395			
C	182	295 AREA 1	65	90	15	250	335 AREA 4			
B	125	100	108	50 AREA 3	45	225	495			
A	75	245 AREA 2	330	2010	82	310	105			

Fig. 2.—Total time (minutes) spent by belled animal in each square, for monthly observations from April 1952 to October 1952 inclusive.

Each area measured 60 yd by 50 yd. Each of two observers sampled two areas on each sampling day, allocation of area and order of sampling being at random. Three traverses were carried out in each area on each of 19 days, spread over $5\frac{1}{2}$ months. The first traverse occupied the first yard, the second the twentieth yard and the third the fortieth yard, the next sampling covering the 2nd, 21st, and 41st and so on, the object of the spacing being to avoid covering the same larval aggregation with all of one day's traverses. Forward and return traverses were made with the leggings only, after which the 18-in. wide blanket was trailed once over the same transect. Dung pats on each 1-yd wide transect were counted during traversing. Wet ground prevented use of the blanket on areas 1 and 2 on January 28 and February 27, and on area 3 on February 18.

(ii) *Habits of the Cattle*.—Figures 3, 4, and 5 show the routes and distances travelled by the belled animal on nine occasions. Figure 6 shows the percentage of visible animals grazing or walking, as opposed to lying or standing. From these it will be seen that the animals remained lying or standing in the day camp,

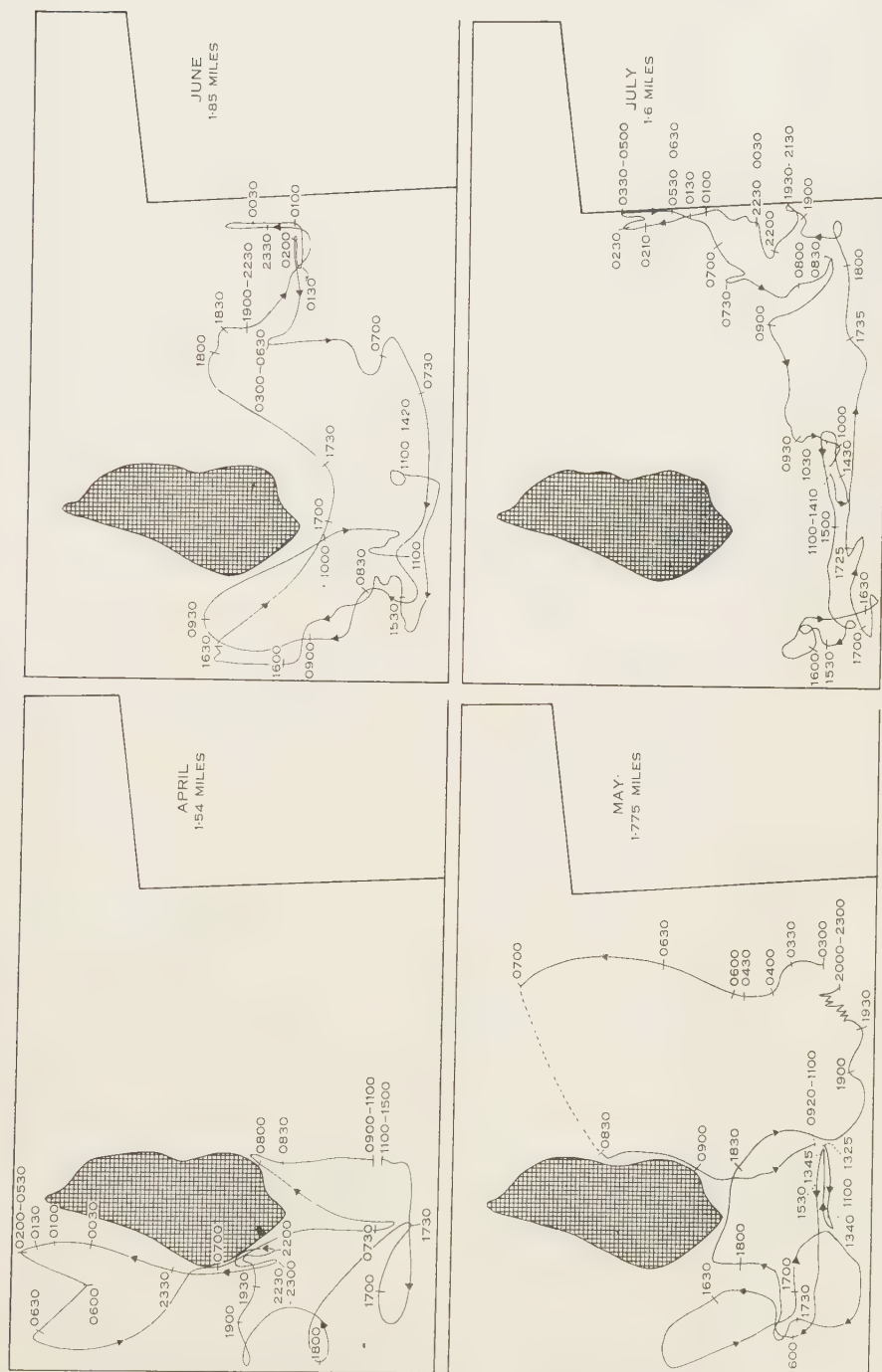


Fig. 3.— Paths followed by belled animal during 24-hour observations of cattle, and distances travelled. Observations started at 11 a.m. on each occasion. April to July observations.

except for some drinking or limited grazing, until between 1.30 and 4.00 p.m., when the afternoon grazing commenced. The period of resting in the camp was longest in hot weather. The afternoon grazing lasted until between 7.30 and 9.30 p.m., when most animals lay down. They commenced grazing again between 11.00 p.m. and 3.00 a.m. and later lay down until sunrise. Night resting places were in the open, away from trees. The cattle regularly commenced grazing shortly after sunrise and continued until 9.00 to 11.00 a.m., when they entered the shade of the day camp, to repeat the cycle. During the hours of daylight it apparently made little difference to the time-table whether the sun was obscured by cloud or not.

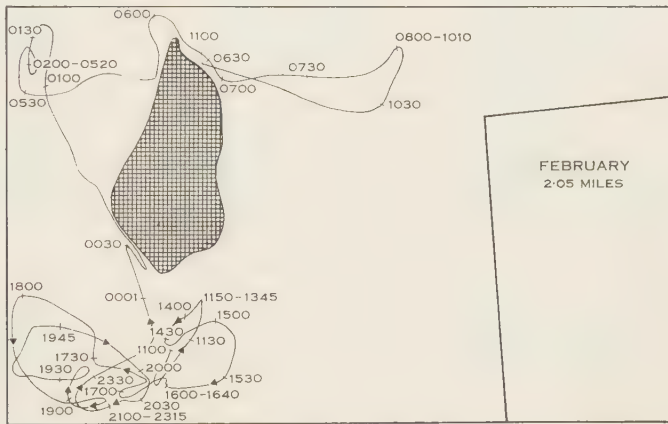


Fig. 5.—Path followed by belled animal during 24-hour observations of cattle, and distances travelled. February observation.

The cattle grazed the flat south-eastern half of the paddock in the afternoon (Figs. 3, 4, and 5) and then commonly moved either to the rising ground of the north-western half, or to the slight rise in the treeless southern corner, for night grazing and resting.

The preference for resting on the higher ground at night may be connected with the well-known observations that high ground is warmer in winter and cooler in summer, compared with hollows, while the thick grass and dryness of the hillside no doubt provided attractive bedding.

(iii) *Catches of Tick Larvae on the Four Areas.*—Area 4 yielded the highest counts of tick larvae (Fig. 7). This area was second lowest in number of "cattle hours". The high correlation between dung pat numbers and cattle hours (Table 10) provides support for the method of assessing the relative times spent by cattle in the areas. Two factors may have contributed to the very high larval infestation in area 4. Firstly, if most adult ticks drop off in the early hours of the morning (see Section I) the hillside would be relatively heavily infested because of its use for night camps and early morning grazing. Secondly, the heavy grass cover provided satisfactory oviposition sites for ticks and may have interfered to some extent with the searching activities of ants.

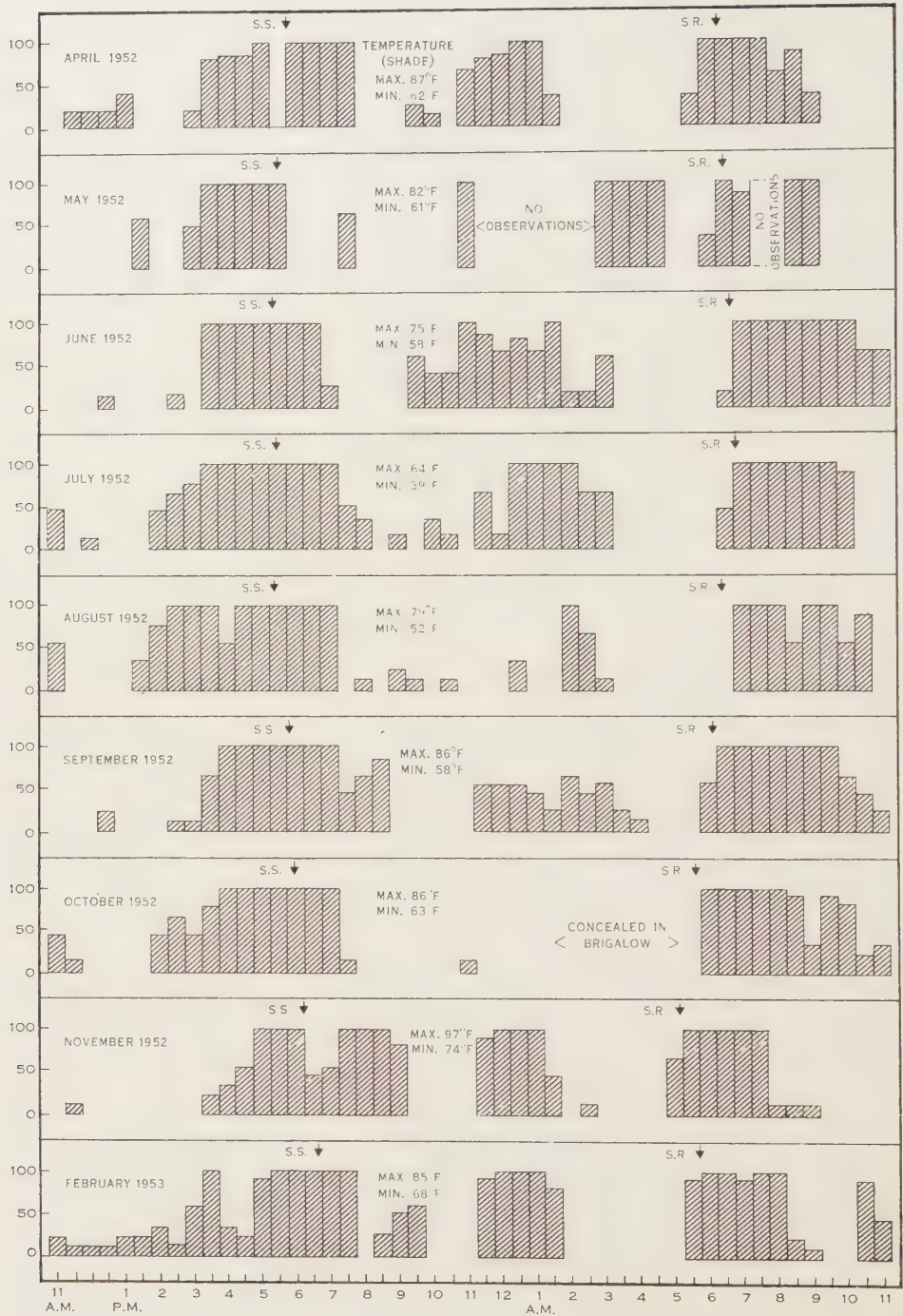


Fig. 6.—Percentage of visible cattle grazing and walking as opposed to lying or standing during 24-hour observations illustrated in Figures 3–5. S.S., time of sunset; S.R., time of sunrise.

Area 2, near the watering place, contributed the second largest number of larvae. The area was well frequented by cattle (Table 10 and Fig. 2), both when drinking and grazing. As in the case of area 4, *Iridomyrmex* nests were not



Fig. 7.—Counts of larvae obtained by sampling four areas of pasture, compared with concurrent larval counts on cattle (sum of counts on flank and dewlap areas). Sampling of areas 1 and 2 omitted on 31.xii.52, of areas 3 and 4 omitted on 7.i.53.

numerous in the immediate vicinity (Fig. 8). Two weeks after the removal of the cattle, relatively high numbers of tick larvae were taken on this area suggesting that the lower earlier counts may have been due to frequent removal of larvae by the cattle, rather than to lack of production of larvae. In contrast, catches of

larvae on areas 1 and 3 did not increase after removal of the cattle suggesting that relatively few larvae were hatching there.

TABLE 10
CORRELATION BETWEEN NUMBERS OF DUNG PATS OBSERVED ON THE LARVAL SAMPLING AREAS, AND TIME SPENT BY ONE OF THE ANIMALS OF THE HERD IN THE AREAS

Area	Dung Pats Observed on Sampling Transects	Time Spent by Belled Animal in Areas (min)*
1	83	222.5
4	154	435.0
2	225	565.0
3	429	1247.0
$r = 0.996; P < 0.01, 2 \text{ d.f.}$		

* Derived from records of minutes spent by this animal in the squares delineated in Figure 2. Figures are averages of the times recorded for the two squares overlapped by each area. Based on observations of cattle habits from April 1952 to February 1953, inclusive.

Area 3 had the highest counts of cattle hours and dung pats, but few larvae were taken. Meat ants could be seen crossing the bare camp area from nearby nests and no doubt they attacked many recently dropped ticks. The sparse grass

TABLE 11
NUMBERS OF CATTLE IN THE 400-ACRE PADDOCK, AND DATES OF DIPPING IN 0.5% (NOMINAL) DDT.
The numbers of days intervening between each dipping are entered between dipping dates

Date and Days Intervening	Cattle Numbers	Date and Days Intervening	Cattle Numbers	Date and Days Intervening	Cattle Numbers
25.x.50	96	18.vi.51	94	25.iii.52	127
26 days		37 days		45 days	
20.xi.50	96	25.vii.51	101	9.v.52	95
25 days		35 days		48 days	
15.xii.50	100	30.viii.51	167	26.vi.52	168
38 days		51 days		57 days	
22.i.51	84	20.x.51	237	22.viii.52	161
32 days		40 days		50 days	
23.ii.51	63	29.xi.51	250	11.x.52	94
45 days		36 days		23 days	
9.iv.51	67	4.i.52	250	3.xi.52	103
37 days		32 days		31 days	
16.v.51	83	4.ii.52	181	4.xii.52	135
33 days		50 days			

over the rest of the area provided little cover for ovipositing ticks, or tick eggs. Meat ant nests were probably more numerous around this area because it was more heavily timbered (Anon. 1956) than the other areas.

Area 1 yielded fewest larvae although the grass cover and proximity of *Iridomyrmex* nests was similar to that in area 2. Table 10 indicates that the area was less frequented by cattle than the others, and grazing there would be mainly in the afternoon and evening, so probably fewer female ticks dropped on this area than on the others. The waterlogging of the area in wet weather may have killed some ticks (Wilkinson and Wilson 1959) and ants other than meat ants may have acted as predators.

The decline in numbers of larvae on all areas between mid November and the end of December is associated with the end of the second summer generation of ticks (Wilkinson 1955). There was fair agreement between catches of larvae during pasture sampling, and counts on selected areas of the flanks and dewlaps of cattle (Fig. 7).

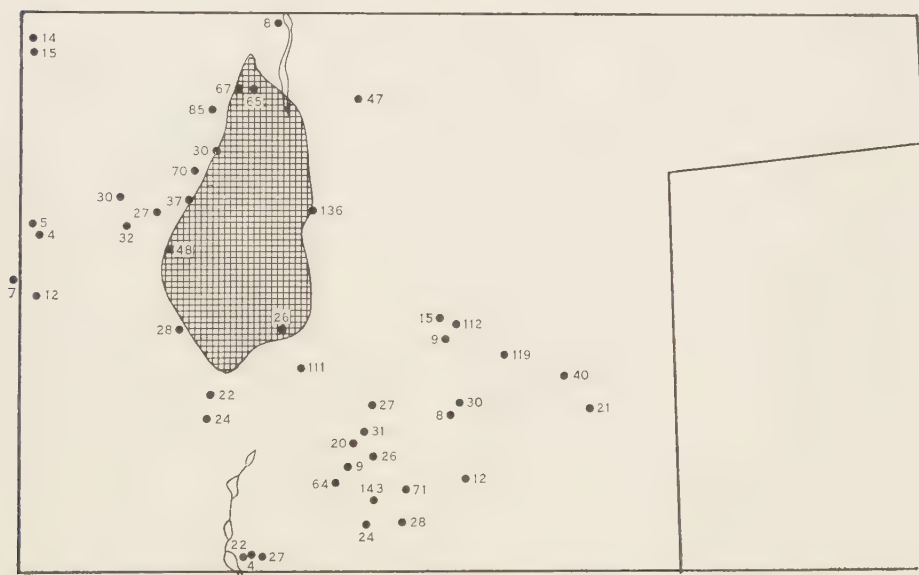


Fig. 8.—Position and number of entry holes of nests of the meat ant *Iridomyrmex detectus* Sm. noted from a horseback survey undertaken on August 6, 1953.

(b) Comparison of Larval Populations on a Creek-bank Plot and a Hillside Plot

(i) *Objects and Methods.*—The observations were carried out in a 400-acre paddock (Fig. 9) used for breeding and fattening Hereford cattle. The numbers of cattle and dates of dipping to control ticks (at the owner's discretion) are shown in Table 11.

The object was to compare seasonal changes in tick infestation on two contrasting areas, area 1 on a creek flat and area 2 on a stony hillside, each area measuring 60 yd by 50 yd.

Most earlier detailed work on the distribution of ticks has been concerned with species of *Ixodes*, and has demonstrated the localized nature of the distribution of these hygrophilic ticks, which are largely confined to situations with a "mat" of moist rotting vegetation at the soil surface. Consequently it was of interest to

determine whether *B. microplus* was similarly dependent on localized favourable vegetation or "mat" layers. The scant published information on the distribution of *B. microplus* in Australia (Seddon 1951) suggests *Boophilus* is not limited in this way, being found in an almost continuous distribution throughout all areas in which climatic conditions are favourable.

The number of cattle and size and hilliness of the paddock precluded detailed observations of cattle habits, but it was known that both areas were well frequented by them. The areas were approximately equidistant from the main "camp" tree (Fig. 9 and Plate 3, Fig. 2) and minor camp trees near the lagoon, where cattle rested during the heat of the day. The cattle drank from the creek and lagoon

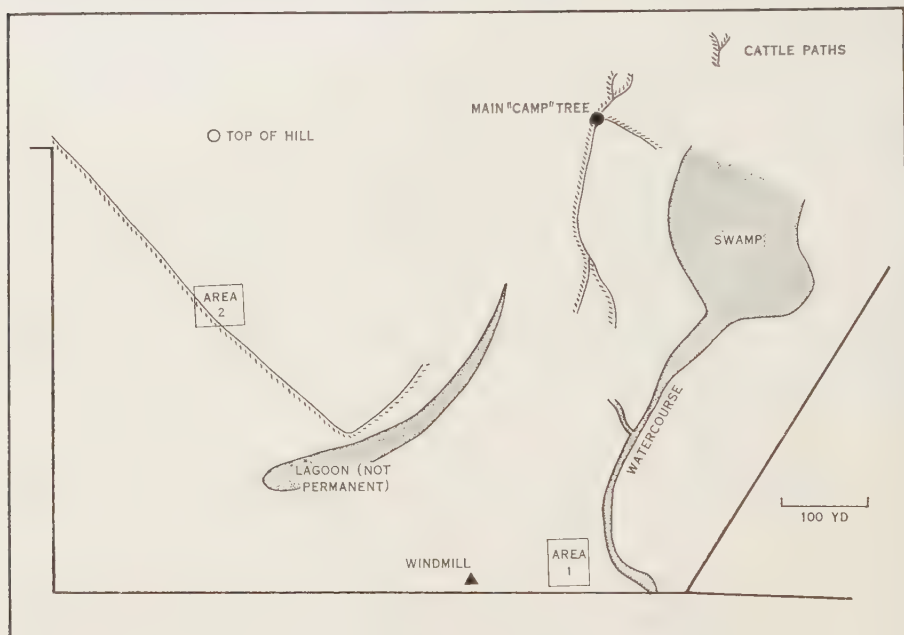


Fig. 9.—Map of part of 400-acre paddock.

and, in 1952, from a trough near the windmill. To obtain further information on the time spent by cattle on the plots, the number of dung pats on each 1-yd wide transect were recorded after each sampling traverse.

More records of dung pat numbers were available than in the 80-acre paddock, since sampling continued for 22 as opposed to 5 months, and these data have been processed with the aim of providing an index of cattle hours spent on the plots. Dung pats were recorded either as fresh — moist and little or no crust, medium — crust formed but still dark, or old — with crust grey and dried. After pats had started to break up they were no longer recorded. For each month the mean number of fresh-plus-medium pats per sampling day was doubled and the mean number of old dung pats per sampling day in the following month was added. The monthly figures thus obtained were smoothed with a three-point moving average and entered in Figures 10 and 11. The object of this treatment

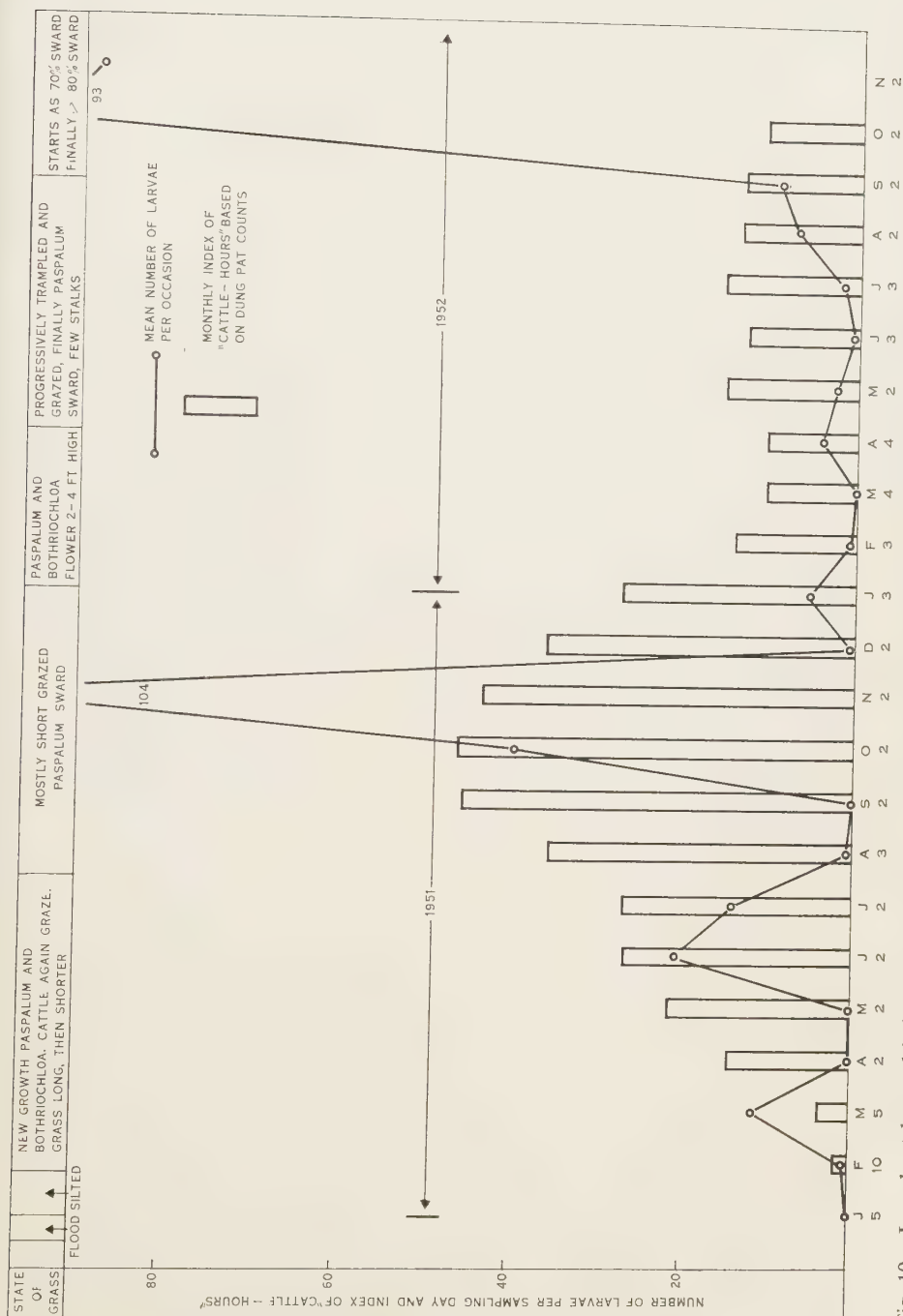


Fig. 10.—Larval catches and index of grazing intensity (derived from dung pat counts) on area 1. Three transects were covered on each sampling day. The numerals under the initial of each month indicate the number of sampling days.

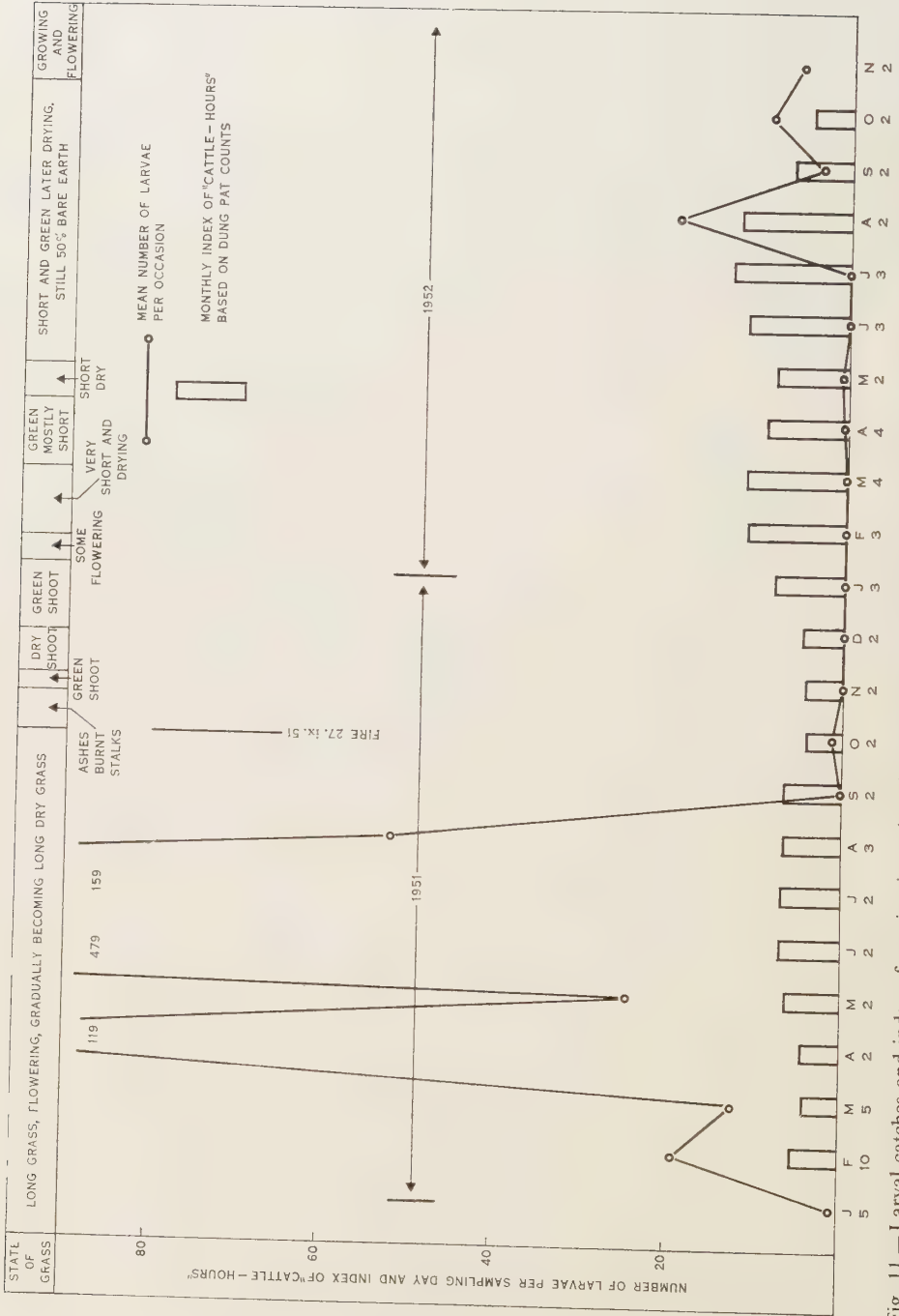


Fig. 11.—Larval catches and index of grazing intensity (derived from dung pat counts) on area 2. Three transects were covered on each sampling day. The numerals under the initial of each month indicate the number of sampling days.

of the data is to give greater importance to fresher dung pats since they can be assumed to have dropped within the last 30 days, whereas the older dung pats, while conventionally regarded as dating from the previous month, may be older. There are a number of possible objections to this index, e.g. variation in weather conditions affects the aging of pats and they are sometimes difficult to see in long grass. However, pending further investigation of its validity, the index appears to provide useful information on major seasonal changes in cattle habits. Cattle defaecate between 7 and 12 times per day (Hancock and McArthur 1951; Bonsma and Le Roux 1953; Laurence 1954).

Information on the vegetation of the areas in March 1951 is summarized in Appendix I and illustrated in Plate 2. On each sampling day notes were made on the height of the vegetation, approximate percentage of ground area covered with vegetation, whether the pasture was green or dry, and the main species flowering. These notes have been summarized at the top of Figures 10 and 11. There is little reason to believe that species composition of the grass affects the distribution of larvae (molasses grass, *Melinis* sp., which is inimical to tick larvae (De Jesus 1934), was not present). Microclimate as affected by the size, habit, and moisture content of the grass plants would be more important.

The path across area 2 (Fig. 9) led from an area of pasture off the map to the watering place at the lagoon. The path did not appear to be heavily infested and limited observations on other cattle paths have not revealed higher infestations than neighbouring pasture. It is therefore considered unlikely that the presence of the path had any noticeable effect on larval numbers recorded in the area.

Before commencing sampling, one observer was allotted to each area at random, and sampling of each area commenced simultaneously. The routine of sampling was similar to that described for the 80-acre paddock, except that in January and February 1951 the three transects sampled in each area each day were adjoining, instead of being separated at 20-yd intervals. When the end of an area was reached with the separated transect system, sampling started again at the three initial positions. The lapse of time between repeated samplings of the same transect was such that transects could be regarded as being hitherto unused, since, particularly in summer, development of tick eggs and death of larvae are comparatively rapid (Wilkinson and Wilson 1959), as is grass growth. In addition cattle crossed the area, removing larvae and renewing the supply of female ticks.

Only the legging samplers were used before October 10, 1951. Thereafter the blanket method was also used on both areas, because the *Paspalum* on area 1 was closely cropped. When the grass became longer, the use of the blanket was continued, to compare the effectiveness of the two devices.

On the three sampling days between October 10 and November 8, a 36-in. blanket was used, but the width was reduced to 18 in. because when larvae were numerous their removal from the pile of the blanket was impracticable, in the time available. Before entering in Figures 10 and 11, catches from the 36-in. wide blanket were divided by four to allow for the difference in area of the two blankets. On the majority of occasions counts on the blanket were lower than on the leggings.

TABLE 12
METEOROLOGICAL DATA RECORDED AT ROCKHAMPTON AIRFIELD DURING THE SAMPLING OPERATIONS IN THE 80-ACRE AND 400-ACRE PADDOCKS
The airfield is 6 miles from the 400-acre paddock and 7 miles from the 80-acre paddock

Month	1951		Rainfall (in.)	1952		Rainfall (in.)	1953 (April)		Rainfall (in.)
	Mean Temperatures (°F)			Mean Temperatures (°F)			Mean Temperatures (°F)		
	Max.	Min.		Max.	Min.		Max.	Min.	
Jan.	86.6	71.5	19.39	92.7	73.9	4.59	86.3	71.3	10.79
Feb.	88.6	77.1	1.25	90.1	72.3	3.47	88.4	71.9	7.18
Mar.	88.2	69.8	1.27	87.3	69.5	3.94	87.1	68.9	3.16
Apr.	87.3	64.0	0	85.7	66.5	1.53	87.2	66.9	1.29
May	80.0	56.6	0.02	78.4	59.5	2.36			
June	76.7	53.7	0.53	74.9	51.1	2.82			
July	75.6	50.9	0.15	74.9	53.2	1.07			
Aug.	78.0	49.4	0.52	78.0	56.7	0.72			
Sept.	82.3	58.0	0.44	81.7	58.9	2.06			
Oct.	89.1	64.4	1.52	84.8	65.1	6.00			
Nov.	93.6	69.7	0.12	92.5	70.6	2.50			
Dec.	95.7	71.7	2.92	93.6	71.6	1.94			

Temperatures and rainfalls recorded at Rockhampton airfield are shown in Table 12.

(ii) *Seasonal Changes in Larval Catches and Vegetation.*—Area 1 was flooded for some time between January 9 and 15 and appeared to be grazed very little during that month, during which the grass was covered with silt. New grass appeared by February 9 and after this date cattle were often seen grazing the area before each sampling. A severe drought developed in the latter part of the year and a fire, which spread from neighbouring property, burnt the hillsides at the end of September. The cattle concentrated their grazing along the creek flats and this is reflected in the high cattle-hours index of area 1 from June 1951 to January 1952 (Fig. 10). The owners added extra cattle in August 1951 (Table 11). After the rains in January 1952, feed was again available on the hills and the *Paspalum* in area 1 flowered. As usual, an ergot developed on the flower heads, and this may explain the low cattle-hours index during February–April 1952.

During the winter of 1952, rainfall was better distributed and winter grazing pressure on the creek banks was less severe than in 1951, but grass on area 1 was again closely cropped by November 1952.

The large peaks in larval numbers in October–November in both years (Fig. 10) were to be expected, since all larvae from ticks dropping between mid July and mid October tend to hatch during these two months. The smaller peaks in larval numbers may be due to chance variations, since only a small proportion of the creek flat area was traversed on each sampling day.

During the first half of 1951, several depressions in the grass, each with a few adjoining dung pats, were seen on area 2. They were not under tree canopies, and this indicated that they were nocturnal resting places, since in daytime British breeds of cattle normally rest in the shade in central Queensland. In June 1951 one of these “lairs” was surrounded by approximately 12,000 larvae (lairs with several hundred larvae each were seen at different times in other parts of the paddock). This use of area 2 for resting at night, and for wet season grazing, no doubt accounted for the large numbers of larvae present in June to August 1951 (Fig. 11). The 12,000 larvae mentioned were reduced to about a tenth of this number by July 5 and were absent on August 15. The fierce grass fire of September 27 left only bare earth, ashes, stones, and a few unburnt stalks (Plate 2, Figs. 3 and 4), but 33 days later one larva was picked up on the leggings and six on the blanket. This short interval suggests either that a female tick survived the fire (e.g. under a stone), or that the bare hillside, warmed by insolation, allowed accelerated development of larvae, from a tick dropped after the fire.

The grass remained very short, with intermittent periods of greenness and dryness until January 1952, when a few plants flowered. Larval catches remained low, with a rise in July and August, which may have been due to increased use of the area by cattle in February–April. A “spring rise” of larvae in October–November was not seen on this plot in either year, perhaps because the scant grass cover provided insufficient dry season shelter for egg development. At the end of the sampling period it was estimated that 30–50% of the area was still bare ground.

IV. DISCUSSION

The hinged flag is one of the most satisfactory forms of sampling device since yield of larvae is comparable to the wheeled sampler, and it is not so cumbersome. The leggings yielded nearly as many larvae as the wheeled sampler per foot frontage but about twice as many traverses would have to be made to yield equivalent numbers of larvae; however, the leggings have the advantage that they can be used in rough and closely timbered country, in fact in most places accessible to cattle. The hinged flag and wheeled samplers are easier to examine than the leggings, and are more readily standardized in method of use. Losses of larvae during examination of the cloth at the end of a transect would be negligible with the hinged flag sampler, since the board is held almost horizontally during counting, or the cloths are removed and placed in tins, with the larvae innermost.* Attempts to motorize the wheeled sampler were not promising, owing to vibration and lack of manoeuvrability.

No attempts were made to utilize the finding that bovine odour (or the effects of rubbing the cloth on the animal) increased retention of larvae. The practice would complicate the procedure and would be difficult to standardize.

Although no effects of time of day of sampling on yield could be demonstrated in South Queensland, this factor may still be important in other climatic regions, for example in hotter, drier regions.

Following the tests described in Section II(c)(iii), the numbers of larvae picked up on individual transects were plotted on a map of the paddock, but no relations between larval numbers and the vegetation, topography, or watering places of the paddock were discernible.

The number of cattle tick larvae in a given area of a continuously stocked paddock will depend on the number hatching and the number removed by animals or death. The most probable interpretation of the differences in larval catches, on the four plots in the 80-acre paddock, is that numbers hatching considerably exceeded numbers removed by cattle on area 4, whereas on area 2 numbers removed were close to numbers hatching, and on areas 1 and 3 few larvae hatched. Of the areas sampled, it appears the cattle picked up most larvae on area 4 or area 2.

The high cattle-hours index and high tick infestation of area 1 of the 400-acre paddock in October and November 1951 illustrated the way in which seasonal concentration of grazing is conducive to heavy tick infestation.

The observation that the creek flats were grazed more heavily in the dry than in the wet season, is complementary to the deductions of Shaw and Bisset (1955) that the reverse tendency occurs in intensity of grazing hillsides. The cattle-hours index of area 2 of the 400-acre paddock was probably not representative of the grazing intensity of ridges because of the use of the area for resting at night and because of the destruction of the grass by fire.

* *Note added in proof.*—Stampa's (1959) method of removing larvae on transparent adhesive tape, which is then placed in a notebook for subsequent counting and identification of the larvae, has proved promising in preliminary trials.

It was obvious that large numbers of larvae were widely distributed in pastures remote from the watering points and day camps. It can be assumed that in larger paddocks they are present as far out from water as cattle will walk. This reduces the economic feasibility of treating the pasture with acaricides, except perhaps in tick eradication campaigns. However, in drier areas, near the geographical limits of tick distribution, ticks may die out where soil moisture is inadequate for egg development (cf. laboratory data of Hitchcock (1955*b*) and Snowball (1957)), and infestations may then be confined to creek and river frontages, or possibly to moist areas around artificial watering points.

Further investigation of the effect of "burning-off" is warranted. It is unlikely to cause a prolonged reduction in pasture infestation by itself, but combined with acaricidal treatment of the cattle or a short period of deferred grazing (Wilkinson 1957), it may be more practicable and effective than either of these treatments separately.

The camp tree (Fig. 3 and Plate 3) was in the centre of an area of bare soil about 14 yd in diameter, much frequented by ants. It appeared unlikely that it was a focus of tick infestation. The same comment applied to the camp in area 3 in the 80-acre paddock, so the suggestion of Bonsma (1944) that cattle are particularly exposed to tick infestation while resting under trees, received no support.

V. ACKNOWLEDGMENTS

Messrs. G. A. McIntyre and K. P. Haydock of the Division of Mathematical Statistics were most helpful in both the planning of some of the trials and interpretation of the results. The Queensland Government Botanist kindly identified the grasses mentioned in Appendix I. Mr. J. T. Wilson provided able technical assistance.

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SAMPLING PASTURES FOR CATTLE TICK LARVAE

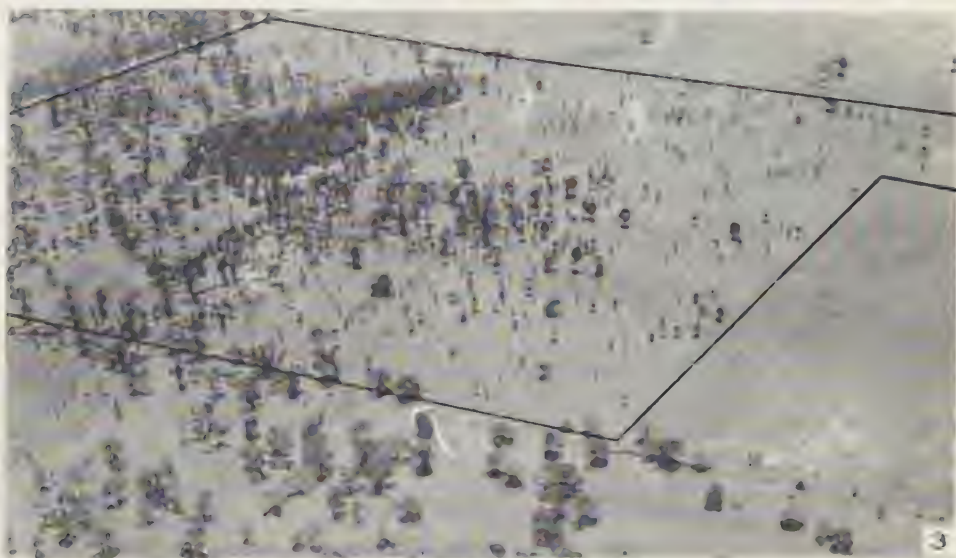


Fig. 1.—The wheeled sampling device.

Fig. 2.—The "hinged flag" in use. Note container for cloth cover on electric fence picket.

Fig. 3.—Aerial view of 80-acre paddock.

SAMPLING PASTURES FOR CATTLE TICK LARVAE

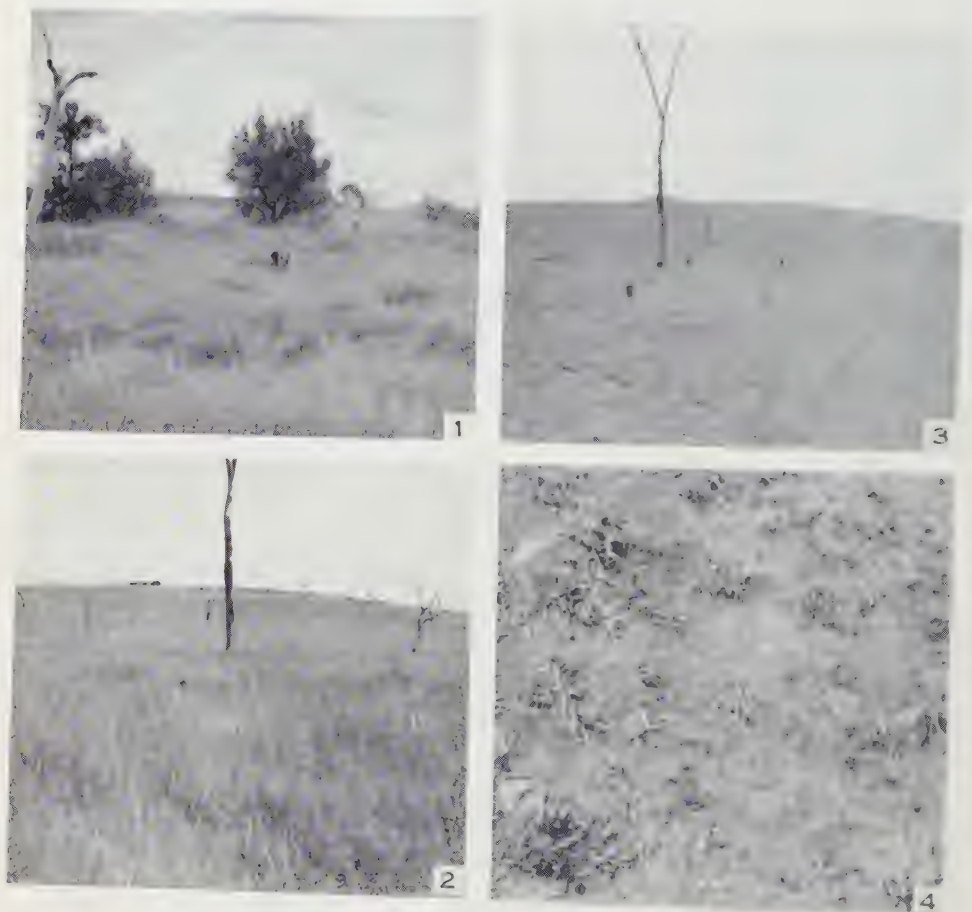


Fig. 1.—Vegetation on area 1, in the 400-acre paddock in March 1951.

Fig. 2.—Vegetation on area 2, in the 400-acre paddock in March 1951.

Fig. 3.—Area 2, November 1951. The vegetation has not recovered from the September fire.

Fig. 4.—Close-up of vegetation on area 2 to show ground coverage. November 1951. Length of grass blades is 4 in. or less.

SAMPLING PASTURES FOR CATTLE TICK LARVAE



Fig. 1.—The “day camp” of the cattle in the 80-acre paddock.

Fig. 2.—The “camp tree” referred to in Figure 9. Rule marked at 6-in. intervals.



APPENDIX I

VEGETATION OF THE AREAS IN THE 400-ACRE Paddock IN MARCH 1951

Area 1.—The main grasses were *Paspalum dilatatum* Poir, *Bothriochloa intermedia* (R.Br.) A. Camus, *Arundinella nepalensis* Trin., *Chionachne cyathopoda* F. Muell. *Paspalum* covered over 80% of the area. Six conspicuous clumps of *A. nepalensis* were over 6 ft high. The main weed infestation consisted of four clumps of *Xanthium pungens* Wallr., height 42 in., and a few dead unidentified thistles, height 48 in. The height of the *Paspalum* leaf blades and seed heads varied from 18 to 36 in. over the area. There was a mat-like (Milne 1950b) formation of rotten vegetation about 2 in. deep over the soil.

Area 2.—The main grasses were *Heteropogon contortus* (L.) Beauv., ex Roem. & Schult., *Chloris ventricosa* R.Br., *Bothriochloa intermedia*, *Panicum decompositum* R.Br., *Sporobolus elongatus* R.Br., *Eriochloa procera* (Retz) C. E. Hubbard, and a sedge, *Cyperus* sp. There was very little or no mat. Bare earth and stones were readily visible over parts of the area. Areas of long (39–54 in.), intermediate (22–30 in.), and short (9–23 in.) vegetation could be distinguished.

CYTOGENETICS OF THE GRASSHOPPER *MORABA SCURRA*

VI. A SPONTANEOUS PERICENTRIC INVERSION

By M. J. D. WHITE*

[Manuscript received August 4, 1961]

Summary

A single individual of *Moraba scurra* from Michelago, N.S.W. (out of 1730 examined cytologically) was found to be heterozygous for a pericentric inversion, which has converted the normally equal-armed *AB* chromosome into a J-shaped element with one limb about twice the length of the other. This is presumably a newly arisen rearrangement. It leads to five detectable cytogenetic consequences: (1) a decline in the chiasma frequency of the *AB* bivalent; (2) occasional failure of pairing, there being two *AB* univalents at first metaphase; (3) frequent orientation of the *AB* bivalent with its centromeres on the equator instead of in the axial plane; (4) frequent formation of a chiasma between the mutually inverted sections; (5) a stimulatory effect on the chiasma frequency of the short arm of the *CD* chromosome carrying the Blundell inversion. The implications of these findings for the chromosomal evolution of the approximately 180 known species of morabine grasshoppers are indicated.

I. INTRODUCTION

In the course of work on the cytogenetics of the wingless eumastacid grasshopper *Moraba scurra*, the chromosomes of over 13,000 male individuals from natural populations have been examined (White 1956, 1957a, 1957b, 1957c; White and Chinnick 1957; Lewontin and White 1960; White and Andrew 1960, and later unpublished work). It was not surprising that a few of these individuals proved to be heterozygous for unique and hence, presumably, newly arisen chromosomal rearrangements, which have never been encountered again. Some of these were figured in an earlier paper (White 1956). Since we study only the testis, the observations being made almost entirely on first metaphases, it is seldom possible to be certain whether a unique rearrangement is present throughout all the tissues of the individual carrying it; in fact, in a number of instances chromosomally mosaic individuals have been encountered, in which the rearrangement was only present in some of the first metaphases in the testis, but not in others.

Many of the rearrangements that have been seen are translocations of various kinds. Some of these have proved impossible to analyse, while others are quite straightforward. The present paper deals with a pericentric inversion in the large *AB* chromosome, which normally has two limbs which are almost exactly equal in length. The *AB* chromosome as such is not known to show balanced polymorphism for pericentric inversions, either in *M. scurra* or in 110 other species of morabine grasshoppers in which it can be recognized as a member of the karyotype; however, in those species in which the *AB* has become "dissociated" into acrocentric "*A*" and "*B*" elements one or other of these is frequently polymorphic for a pericentric inversion.

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II. OBSERVATIONS

In approximately 156 first metaphases in a testis squash preparation made from an individual of *M. scurra* collected at Michelago, N.S.W. ("Michelago 955") one of the *AB* chromosomes is normal (i.e. equal-armed) while the other has one limb about twice the length of the other. The overall length of the two homologs appears to be the same, so that if we are not dealing with a 3-break rearrangement (which is implausible) a pericentric inversion must have occurred (Fig. 2(a)).

In 133 cells (Table 1) the two *AB*'s are associated by a terminal chiasma involving the long arm of the inversion-carrying homolog (Fig. 1(a)); no cells in which the *AB* has a single chiasma involving the *short* arm were seen. However, two cells were seen in which the *AB* has two terminal chiasmata; in this case it has a characteristically lop-sided appearance (Fig. 1(b)).

TABLE 1
CHIASMA FORMATION IN THE *AB* PAIR OF INDIVIDUAL "MICHELAGO 955"

	No. of Cells Observed
A single distal chiasma (Fig. 1(a))	133*
Two chiasmata, both terminal (Fig. 1(b))	2
Two chiasmata, one in inverted segment (Fig. 1(c))	19
One chiasma, in inverted segment	1 (?)
One chiasma, in short arm of inverted chromosome	0
Two univalents (Fig. 1(f))	1
Total	156

* In 30 of these the *AB* bivalent is more or less maloriented and in 18 of those 30 it has both centromeres located on the equator.

In 19 cells the *AB* bivalent shows, in addition to the usual distal chiasma, one in the inverted region. Such a bivalent is shown in Figure 1(c) and is interpreted in Figure 2(c). Such bivalents prove that, at least occasionally, a "reversed loop" is present at pachytene.

In the bivalents with a single terminal chiasma the centromeres are further apart than they would be in a normal *AB* bivalent, even one of those very rare ones with but one chiasma. Probably as a result of this the structurally heterozygous *AB* bivalents rather frequently become orientated at first metaphase with both their centromeres exactly on the equator, instead of in an axial plane (Fig. 1(e)). This is the type of behaviour also shown in one cell with two *AB* univalents (Fig. 1(f)). Other less regular types of malorientation also occur.

What the fate of these maloriented *AB* bivalents would be cannot be determined, since first anaphases and second divisions are not present in the preparation.

One cell (Fig. 1(d)) shows a unique peculiarity in that the *CD* bivalent, heterozygous for the Standard/Blundell sequences, has *two* terminal chiasmata, both of which are presumably outside the inverted region. This is the only bivalent of this type that we have seen in five years' work on *M. scurra* in the

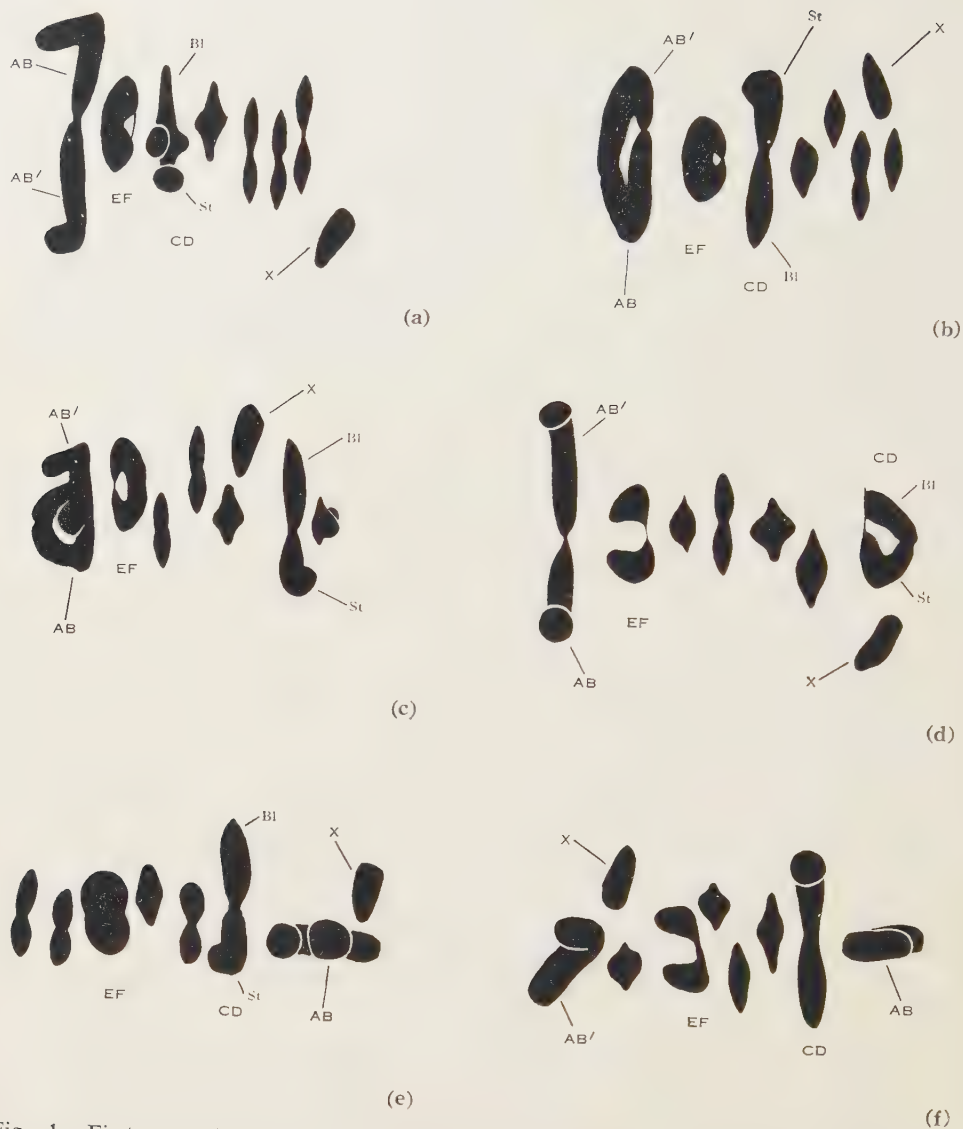


Fig. 1.—First metaphases (in side view) of "Michelago 955". This individual was heterozygous Blundell/Standard for the CD chromosome and homozygous Standard/Standard for the EF chromosome. AB, the normal AB chromosome, AB', the one carrying a pericentric inversion: (a) with a single terminal chiasma in the AB bivalent; (b) with two terminal chiasmata, one in the inverted segment; (c) with two chiasmata, one in the AB bivalent and two chiasmata in the CD bivalent; (d) with one terminal chiasma in the AB bivalent which is bent into a horseshoe-shape and orientated with both centromeres on the equator; (e) with separate AB and AB' univalents.

course of which many tens of thousands of St/Bl bivalents have been seen. Its presence in an individual heterozygous for a unique rearrangement in another chromosome pair is hardly likely to be fortuitous; it seems far more likely that

heterozygosity for the inversion in the *AB* has a stimulatory effect on chiasma formation in the *CD* bivalent of a type well known in *Drosophila* (Schultz and Redfield 1951) and for which there is statistical evidence in other species of grasshoppers (White and Morley 1955).

III. DISCUSSION

The behaviour of this pericentric inversion is very different from that of most such rearrangements which have established themselves in a balanced polymorphic condition in grasshopper populations. In the case of the *CD* and *EF* bivalents of *M. scurra* heterozygosity for the long established Blundell, Molonglo, Snowy, and

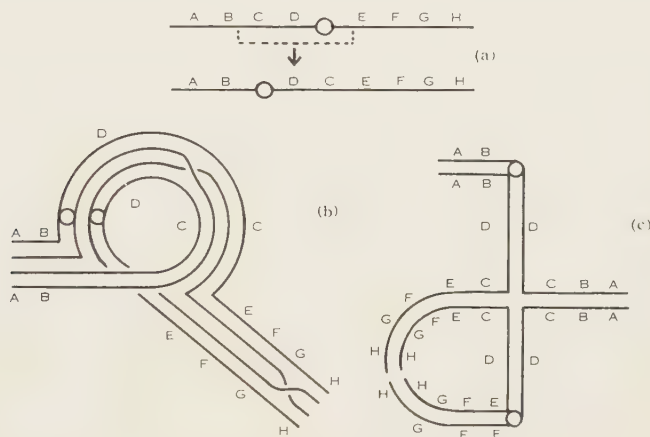


Fig. 2.—(a) Diagram of the pericentric inversion showing its approximate limits; (b) pachytene diagram; (c) first metaphase diagram of the bivalent seen in Figure 1(c).

Tidbinbilla pericentric inversions is not accompanied by formation of chiasmata within the limits of the inversions or by malorientation of the bivalents. And in the many North American grasshopper species belonging to the genera *Trimerotropis*, *Circotettix*, and *Aerochoreutes* numerous polymorphisms involving pericentric inversions exist in the natural populations without chiasmata being formed within the inverted segments. One exception has, however, been recorded. That is in *Trimerotropis sparsa* where a few individuals at Cherry Creek, Nevada, and Beaver, Utah (White 1951; White and Morley 1955) have shown such chiasmata within the limits of an inversion; in that case one of the homologs is metacentric, the other J-shaped, whereas in the case of the *AB* bivalent of “Michelago 955” one element is equal-armed, the other J-shaped.

The genetic significance of a chiasma within the limits of a pericentric inversion is that it leads to the production of gametes having a duplication and a deficiency. Thus heterozygotes for pericentric inversions which form such chiasmata will have their fertility more or less severely reduced. This is, no doubt, the reason why pericentric inversions are almost unknown in the polymorphic state in

Drosophila populations and have only played a very minor part in *Drosophila* phylogeny (Stone 1955). Many trimerotropine and morabine grasshoppers escape "paying the penalty" for pericentric inversions because they simply do not form chiasmata within the inverted region, even though this segment may have quite a high chiasma frequency in the homozygous, inverted or non-inverted, condition (White and Morley 1955). Observations on pachytene are extremely difficult to make in these species, but apparently bivalents heterozygous for pericentric inversions simply do not form reversed loops; instead the inverted and the non-inverted pair "straight", i.e. non-homologously (Coleman 1948; and unpublished observations of the present author on rather unsatisfactory preparations of various species). These conditions have permitted the development of elaborate systems of cytological polymorphism in these insects, which could not have persisted if any considerable number of chiasmata were formed in reversed loops. Just how the "Sevier" inversion in *T. sparsa* manages to persist at two localities in the Great Basin of North America in spite of the fact that it occasionally forms such chiasmata is unknown: possibly heterosis is very strong in this case.

The significance of the newly arisen pericentric inversion in "Michelago 955" is, precisely, that its behaviour and properties have not been modified by natural selection, as must have happened in the case of all inversions that have been established in a natural population for many generations. Clearly, it does show "reversed loop pairing", at any rate in a certain percentage of cells; and may form a chiasma within the loop. This, in itself, would reduce fecundity quite seriously. But it may be that the tendency of the structurally heterozygous *AB* bivalent to be malorientated on the spindle — even to the extent of having both its centromeres on the equator — would be an even more serious cause of infertility. This failure of co-orientation of the centromeres is an extremely interesting phenomenon in itself; it presumably arises because they are further apart than they would ever be in a normal bivalent, even one of those rare ones which have a single terminal chiasma in one arm and none in the other. If there is any truth in Östergren's (1951) "co-orientation by pulling" hypothesis, we might say that the distance between the centromeres is too long (in relation to the dimensions of the spindle) for the pull to be effective.

A large metacentric corresponding to the *AB* is known to exist in 110 species of morabine grasshoppers without there being any evidence of pericentric inversions having established themselves in it in the whole course of its phylogeny (White, unpublished data). On the other hand, in a further 38 species the *AB* is dissociated into two constituent acrocentric elements "*A*" and "*B*" (there have been approximately 13 different evolutionary dissociations of the *AB*). And in at least 7 of these 38 species one or more pericentric inversions *have* managed to establish themselves in either the *A* or the *B* chromosome in a polymorphic condition; while in a number of others pericentric inversions in *A* or *B* seem to have reached fixation.

Clearly then, it is not the nature of the genetic material in the *AB* which precludes it from successfully undergoing pericentric inversion; rather, it is its dimensions which impose this limitation on its evolutionary potentialities. If any

pericentric inversions at all have managed to establish themselves in the phylogeny of the *AB*, they must have been of cytologically undetectable types (i.e. either very small or else with the breaks equidistant from the centromere).

We may conclude that malorientation rather than chiasmata in the reversed loop is the main factor that has prevented pericentric inversions from establishing themselves in the *AB* chromosome of the morabine grasshoppers. All newly arisen pericentric inversions probably have a certain frequency of formation of chiasmata in reversed loops but this may have been rapidly reduced by natural selection to zero in the case of such "successful" inversions as the Blundell and Tidbinbilla inversions of *M. scurra*. The Sevier inversion of *Trimerotropis sparsa* may represent a relatively recent rearrangement — or perhaps the Sevier/Standard heterozygous combination at Cherry Creek and Beaver results from recent mixture of populations homozygous for those gene sequences.

The great majority of the pericentric inversions which have established themselves in grasshopper populations have done so in chromosomes that were originally acrocentric, i.e. they have tended to decrease the intercentromeric distance in the meiotic bivalent, thereby increasing the "safety factor" as far as co-orientation on the spindle is concerned. It is interesting to note that almost the only pericentric inversions known to have established themselves in metacentric chromosomes in the genus *Drosophila* (the 3 *L-R* and 2 *L-R* inversions in *D. robusta*) both have the breakage points almost exactly equidistant from the centromere (Carson 1958). No doubt the formation of chiasmata in reversed loops is the main barrier to the establishment of pericentric inversions in *Drosophila*, but it is possible that malorientation where the intercentromeric distance has been increased may be an additional factor in some cases.

IV. ACKNOWLEDGMENTS

I am extremely grateful to Mrs. J. Cheney, who made the preparation and first detected the *AB* inversion in "Michelago 955". I am also grateful to Professor H. L. Carson for reading the manuscript and making some suggestions.

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TRICHOSTRONGYLES FROM RODENTS IN QUEENSLAND, WITH
COMMENTS ON THE GENUS *LONGISTRIATA* (NEMATODA:
HELIGMOSOMATIDAE)

By PATRICIA M. MAWSON*

[Manuscript received April 21, 1961]

Summary

Trichostrongyles have been studied from 85 rats belonging to eight species, of which two were from south Queensland and the rest from north Queensland, near Innisfail. Parasites identified from the intestine of the host are: Heligmosomatidae: *Nippostrongylus brasiliensis* (Travassos) from *Rattus rattus*, *R. norvegicus*, *R. conatus*, *R. assimilis*; *Longistriata melomyos*, sp. nov., from *Melomys cervinipes*, *M. lutillus*, *Uromys caudimaculatus*; *L. uromyos*, sp. nov., from *Uromys caudimaculatus*; *L. brachybursa*, sp. nov., from *M. cervinipes*, *M. lutillus*; *L. polyrhabdote*, sp. nov., from *R. assimilis*, *M. lutillus*; *Heligmonoides mackerrasae*, sp. nov., from *M. cervinipes*, *M. lutillus*, *U. caudimaculatus*; *H. emanuelae*, sp. nov., from *R. assimilis*, *R. conatus*; *Austroheligmonema typicum*, gen. et sp. nov., from *R. assimilis*; *A. magnum*, gen. et sp. nov., from *R. assimilis*, *R. conatus*, *R. rattus*, *R. norvegicus*, and *M. cervinipes*; Trichostrongylidae: *Austrostrongylus hydromyos*, sp. nov., and *Peramelistrongylus skedastos* Mawson from *Hydromys chrysogaster*.

Two species (Trichostrongylidae) are described from the liver and peritoneum of the host: *Hepatojarakus fasciatus*, sp. nov., from *R. assimilis* and *R. conatus*, and *H. pycnofasciatus*, sp. nov., from *R. assimilis* and *M. lutillus*; *Mastonema melomyos*, gen. et sp. nov. (Heligmosomatidae), is described from the mammary gland of *M. lutillus*.

A key is given to genera related to *Longistriata* Schulz and one to *Longistriata* spp. Notes are made on the definition of the genera *Heligmonoides* Baylis and *Heligmonina* Baylis; *H. stellenboschius* (Ortlepp) and *H. vogeli* Khalil, both previously attributed to *Heligmonoides*, are considered to belong to *Heligmonina*. The genera *Nippostrongylus*, *Trifurcata*, *Tricholinstowia*, *Heligmonoides*, *Heligmospiroides*, *Heligmonina*, and *Longistriata* are considered to form a natural group, to which belong also *Austroheligmonema* and *Mastonema*, and another new genus, *Heligmobaylisia*, which is proposed for the species *Heligmonella jugatispiculum* Sadvovskaya, *H. streptocerca* Baylis, and *H. vladimiri* Sadvovskaya. *Longistriata cameroni*, nom. nov., is proposed for *L. cristata* Cameron non Geddoelst.

INTRODUCTION

The nematodes discussed in this paper were collected by members of the Queensland Institute of Medical Research in the course of work at Innisfail in north Queensland. The worms were kindly loaned to the author for examination by Dr. M. J. Mackerras of that Institute. It provides the first opportunity for examining trichostrongyles from native Australian rodents. By far the greater

* Zoology Department, University of Adelaide.

TABLE 1

NEMATODES RECORDED IN THIS PAPER, ARRANGED TO SHOW LOCALITIES AND NUMBERS OF EACH HOST INFECTED. The numbers indicate how many host specimens were found to be infected with each species of parasite; numbers in the first line indicate total numbers of each host species from which trichostrongyles were taken

Nematode	<i>Rattus rattus</i>		<i>Rattus norvegicus</i>		<i>Rattus conatus</i>		<i>Rattus assimilis</i>		<i>Melomys lutillus</i>			<i>Melomys cervinipes</i>		<i>Melomys</i> sp.*			<i>Uromys caudimaculatus</i>	<i>Hydromys chrysogaster</i>
	Barile Frère	Innisfail	Innisfail	Innisfail	Innisfail	Innisfail	Innisfail	Mossman	S. Qld.	Innisfail	Whyanbeel	Daintree	Miallo	Innisfail	Whyanbeel	Daintree	Carins	Innisfail
Trichostrongyles	1	4	2	8	16	1	3	10	4	4	1	14	1	1	1	1	7	6
<i>Nippostrongylus brasiliensis</i> (Trav.)	1	3	1	8	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Austroheligmonema typicum</i> , gen. et sp. nov.	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
<i>A. magna</i> , sp. nov.	—	1	1	1	14	1	—	—	—	—	—	3	—	—	—	—	—	—
<i>Heligmonoides mackerrasae</i> , sp. nov.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>H. enanae</i> , sp. nov.	—	—	—	6	6	—	—	4	2	1	—	7	—	—	—	—	1	—
<i>Longistriata melomyos</i> , sp. nov.	—	—	—	—	—	—	—	9	2	4	1	14	1	1	1	1	6	—
<i>L. uromyos</i> , sp. nov.	—	—	—	—	—	—	—	1	—	—	—	8	—	—	—	—	6	—
<i>L. brachybursae</i> , sp. nov.	—	—	—	—	—	2	—	—	—	1	—	—	—	—	—	—	—	—
<i>L. polyrhabdote</i> , sp. nov.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Mastonema melomyos</i> , gen. et sp. nov.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hepatojarakus pycnofasciatus</i> , sp. nov.	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>H. fasciatus</i> , sp. nov.	—	—	—	1	2	—	1	1	—	—	—	—	—	—	—	—	—	—
<i>Austrostrongylus hydromyos</i> , sp. nov.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Peramelistrongylus skedastos</i> Mawson	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Heligmosomatidae, unidentified females	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1

* Young animals (either *M. lutillus* or *M. cervinipes*)—too young for identification.

number of parasites, in species as well as numbers, belong to the Heligmosomatidae, a family well-established in rodents all over the world. The finding of these genera and species in Australian rats (the first records of the family in the native Australian fauna) is in agreement with the view, expressed by Chabaud (1959) that the Heligmosomatidae differentiated from the Trichostrongylidae after the geographic segregation of Australian marsupials. It was later that rats arrived in Australia by various routes and at different times. The genera *Melomys*, *Uromys*, and *Hydromys*, and as well as *Rattus assimilis* and *R. conatus*, are considered (Tate 1951) to have appeared relatively recently, possibly by early Pleistocene times, although other groups of native rats were already established before this. *R. rattus* and *R. norvegicus* have been introduced by white man in the last two hundred years or so.

The incidence of the different species of trichostrongyles in the rodent hosts is shown in Table 1. Information available to me unfortunately does not include the proportion of rats infected with trichostrongyles, nor whether other rodent species were dissected and found to be uninfected. The table, however, indicates a distinct difference in the fauna of the three groups: (1) *Rattus* spp., (2) *Melomys* spp. and *Uromys* sp., and (3) *Hydromys* sp. The parasites from, as well as the food and habitat of, *Hydromys* are completely different from those of the other two groups, but the differences between groups (1) and (2) appear to coincide only partly with variation in habitat and food of the host. Some information on the biology of the rat has kindly been given to me by Dr. J. L. Harrison, Queensland Institute for Medical Research (personal communication), who is studying them at Innisfail, and some discussion of their habits has been published by McDougall (1944) who observed them in the cane-fields in north Queensland.

It is hoped that further collections will be obtained from other parts of Australia, so that a comparison of their endoparasites may be made. Until this is done on an extensive scale, no comments can usefully be made on the distribution and relationships of the Australian trichostrongyles. A catalogue of the helminths previously recorded from rodents has been compiled by Mackerras (1958); the collections listed in this work under the rodent hosts as "Trichostrongylidae, undescribed species" are some of those which are identified below.

All the rats from which parasites were obtained were taken direct from the field; none were kept in captivity before dissection.

Measurements.—The measurements and proportions commonly used for comparisons between species have been set out in comparative tables, and are not repeated in the text. In the case of coiled species, and those with inflated or ridged cuticle, breadth measurements have not been given as this is not accurate.

Type material.—The holotype male and allotype female of new species described in this paper have been placed in the South Australian Museum; paratype material is in the collection of the Queensland Institute of Medical Research and in the Helminthological Collection, Zoology Department, University of Adelaide. In the lists of hosts and localities at the head of each description, the type host and locality are placed first.

ventral alae, and some with 1 ala, dorsal, ventral, or lateral. There are also species in which the bursa is symmetrical (the most common form) and a few in which it is slightly asymmetrical either in size of the lobes and rays, or, very rarely, in the form of the rays.

Closely associated with *Longistriata* are a number of genera which appear to form three series in respect of these main differentiating features. These series, or trends, are as follows:

(1) *Cuticular Specialization*.—In *Pudica*, and in a new genus proposed below, *Heligmobaylisia*, paired lateral alae are well developed; in *Heligmonina*, *Heligmospiroides*, *Trichotravassosia*, *Fuellebornema*, and *Evandroia*, 1 ala, lateral or ventral, is prominent. In *Squamostrongylus*, *Heligmostrongylus*, *Heligmodendrium*, *Trichotravassosia* and *Brevistriata*, and in *Acanthostrongylus*, still further cuticular specialization has taken place.

(2) *Bursal Asymmetry*.—Asymmetry of the bursa which when present in *Longistriata* spp. is very slight, is marked in *Heligmonoides*, *Heligmonina*, *Heligmospiroides*, and *Heligmobaylisia*, extensive in *Nippostrongylus*, *Trichobaylisia*, *Mirandaia*, and in two new genera proposed below, *Austroheligmonema* and *Mastonema*, and is extreme in *Oswaldonema* and *Heligmoskrjabinia*.

(3) *Development of the Dorsal Ray*.—The dorsal ray is very insignificant in *Heligmosomum* and *Adolpholutzia*. These two genera, with *Nippostrongylus*, *Trifurcata*, and *Tricholinstowia*, were placed by Skrjabin *et al.* (1952) in the subfamily Heligmosomatinae, characterized by the presence of a very short dorsal ray. In the last three of these, the dorsal ray is in fact no shorter than in some species of *Longistriata*, e.g. *L. depressa*, *L. convoluta*.

In a recent monograph on the Heligmosomatidae, Skrjabin, Shikhobalova, and Schulz (1954) divide the genera among four subfamilies which are separated by the following key, in which comments in square brackets are my own:

- 1 (2). Longitudinal striae absent (except in *Morganiella*); spicules short, more or less massive Viannaiinae
- 2 (1). Longitudinal striae present; spicules long, slender. [This not true of *Adolpholutzia*.]
- 3 (4). Bursa asymmetrical with rays of left and right sides entirely different Oswaldonematinae
- 4 (3). Bursa symmetrical or asymmetrical, but rays of left and right side similar in shape.
- 5 (6). Dorsal ray small, not reaching bursal edge; female tail with terminal spike. [Spike not present in all species attributed here, and is present in some others, e.g. *Murielus harpespliculus*.] Heligmosomatinae
- 6 (5). Dorsal ray longer, reaching to, or nearly to, bursal edge; female tail without a spike Longistriatinae

This classification does not recognize the fact that genera of the last three of these subfamilies are more closely related to each other than to those of Viannaiinae. It also seems that the genera grouped by these authors as tribe Squamostrongylea in subfamily Longistriatinae are at least as distinct a group as those placed as a separate subfamily Oswaldonematinae. According to the key above, *Nippostrongylus* (actually included by the authors in Heligmosomatinae)

would fall into Oswaldonematinae as would *Austroheligmonema* and *Mastonema*; in fact these genera are, in bursal complexity, intermediate between *Trichobaylisia* and *Oswaldonema*, which the authors place in Longistriatinae and Oswaldonematinae respectively.

More recently, Chabaud (1959) has proposed a modified classification for the whole Trichostrongyloidea, based on five points: cuticular development on the head region, number of points on the female tail, the development of the dorsal ray, and, of lesser importance, the type of spicule and the number of uteri. In discussing the type of dorsal ray and the number of points on the female tail, Chabaud takes into consideration recent studies by Osche (1955, 1958). He indicates that the more primitive features are the presence of 3 cones on the female tail, of a buccal capsule or other cephalic chitinization, and of a long dorsal ray, more particularly with the dorsal ray well developed anterior to the origin of the externodorsal ray. Chabaud gives five types of dorsal ray, three types of anterior end, three types of female tail, and two types of spicules, and classifies all genera of the order accordingly.

In using this classification and the accompanying set of values for each character, some difficulty is experienced, partly because five types of dorsal ray and three types of female tail are not enough to express the variations met with, and allows room for objective rather than absolute assessment of the characters.

There are at least two types of female tail in which there is "une pointe unique", those in which the conical tail ends in an acute and sometimes elongate tip (e.g. *Austrostrongylus*, *Trifurcata*) and those in which the tail is less conical, rounded distally, with a slender terminal spike or thread* (e.g. *Nicollina*, *Asymmetracantha*, *Delicata*). Either type is sometimes associated with 2 or more, more or less significant, subterminal cones (*Allintoshius*), and a tail with 3 cones often also carries a thread-like spike.

The five types of dorsal ray, indicating stages in its reduction or longitudinal division, do not allow for a form such as *Nippostrongylus brasiliensis*, in which the shape of the ray is similar to type 1 and its length as type 3 (Chabaud 1959, p. 475). Chabaud allots it to type 3, I consider it nearer to type 1.

In the development of the buccal capsule, also, a difference of judgment can be shown. Two Australian genera, *Nicollina* and *Nycteridostongylus*, are placed by Chabaud in the Anoplostrongylinae, although a well-developed buccal capsule is present. In this case (and possibly in many others) the different viewpoint is due to poor figures of the species, and slight ambiguity in the descriptions.

These points indicate a necessity for modification, or at least elaboration, of Chabaud's outline, and a clarification of the characters of some existing genera. The classification, however, is the most natural, constructive, and interesting so far proposed for the trichostrongyles. The synonymy involved is sweeping, and before its adoption further consideration of some characters is necessary.

* Dr. Chabaud has indicated (personal communication) that this is the shape indicated by "pointe unique" — or Q2.

During the present study of Queensland Heligmosomatidae a key has been made to the heligmosomatid genera, and this is given below. Two genera have been omitted, *Neoheligmonoides* and *Heligmodentostomum*, as their descriptions (as far as they are available to me) are inadequate in respect of the main characters. Both are apparently readily recognizable, the former by the shape of the spicules, and the latter (of which the male has not been described) by the presence of a buccal tooth. The genus *Nematospiroides* Baylis is retained, the character separating it from *Heligmosomum* Raillet & Henry is indicated in the key. Many of the genera recognized are placed as synonyms by Chabaud, since he admits neither cuticular structures (except on the head) nor bursal asymmetry (unless extreme) to be of generic importance. Of the seven genera at the end of the key, each has distinctive features of cuticle or bursa or both, but each is overlapped by one or more species of *Longistriata*. These genera (with others) are placed by Chabaud as synonyms or subgenera of *Longistriata*. It is a question whether the "overlapping" species should instead be removed from *Longistriata*.

It is clear that the same sort of variation occurs among the genera of Heligmosomatidae as among the species of *Longistriata* but in the genera these variations are carried to greater extremes. *Longistriata* may well be a core from which the species of other genera have evolved. In Figure 1 an attempt has been made to represent the situation graphically. In neither key nor figure is it intended to imply that the major subdivisions indicate the order in which the phylogenetic developments have taken place. The length of the dorsal ray used as a criterion is not strictly comparable with the standards given by Chabaud, in which the point of origin of the externodorsal ray is important. In nearly all the genera involved in this more restricted review the dorsal rays belong to his class 1, with a very few in each of the other four classes, and the same applies to the species of *Longistriata*.

The variation seen in this group are similar to those noted by Darwin in domestic plants and animals, by Witenberg (1923) in the Cyclocoelidae (Trematoda), and by others, zoologists, palaeontologists, and botanists, in other groups. From these studies and in particular from those made by himself and his colleagues on cereals, Vavilov (in Chester 1954) deduced his Law of Homologous Series. Vavilov noted that genetically close species "are characterised by resemblances in their series of heritable forms, and it is observed that the closer species are related genetically, the more exact is the repetition of series of morphological and physiological characters". Species "that are closely related genetically are characterised, consequently, by uniform series of heritable intraspecific variations". This resemblance is repeated on a broader scale among related genera and among families. Vavilov's law indicates a definite plan based on laws of genetic variation in the systematics of each group and of the entire animal — and plant — kingdoms. Vavilov concluded that as more variations (specific and otherwise) are known in a group a definite regularity appears following on the nature of the evolutionary process and that as this plan emerges it is possible to predict the occurrence of parallel forms. Such a plan is broadly indicated for the Heligmosomatidae (excluding Viannaiinae) in Figure 1, and the blank sectors in this diagram may be filled in the future with new species or genera.

KEY TO THE GENERA OF THE FAMILY HELIGMOSOMATIDAE

- 1 (6). Dorsal ray very short, less than a fifth of externodorsal.
- 2 (3). Spicules stout, short, slightly complex *Adolpholutzia* Travassos
- 3 (2). Spicules long and slender, may be bifid.
- 4 (5). Bursa asymmetrical *Nematospiroides* Baylis
- 5 (4). Bursa symmetrical *Heligmosomum* Raillet & Henry
- 6 (1). Dorsal ray at least a third length of externodorsal.
- 7 (10). Dorsal ray completely divided to base, two halves apparently separate.
- 8 (9). Externodorsal rays double *Murielus* Dikmans
- 9 (8). Externodorsal rays single *Pseudoheligmosomum* Travassos
- 10 (7). Dorsal ray not completely divided.
- 11 (42). Bursa strongly asymmetrical in size, or asymmetrical in shape or arrangement of rays.
- 12 (19). Alae present.
- 13 (14). Alae symmetrical *Heligmobaylisia*, gen. nov.
- 14 (13). Alae asymmetrical.
- 15 (16). The only asymmetrical ray is externodorsal *Heligmonima* Baylis
- 16 (15). Other rays may be asymmetrical.
- 17 (18). Ventral rays of left and right sides similar in shape *Heligmospiroides* Ortlepp
- 18 (17). Ventral rays similar on two sides *Trichobaylisia* Travassos
- 19 (12). Alae absent or insignificant.
- 20 (25). Bursal asymmetry involves only size, not relative positions, of rays.
- 21 (22). Spicule tip enclosed in sheath *Stilestrongylus* Freitas, Lent, & Almeida
- 22 (21). Spicule tip not in sheath.
- 23 (24). Bursa and dorsal rays very long *Longistriatoides* Yeh
- 24 (23). Bursa and dorsal ray distinctly short dorsally *Heligmonoides* Baylis
- 25 (20). Bursal asymmetry involves relative positions of rays as well as size.
- 26 (33). Only dorsal and externodorsal rays asymmetrical.
- 27 (28). Left externodorsal ray doubled *Mammanidula* Sadovskaya
- 28 (27). Neither externodorsal ray doubled.
- 29 (32). Both externodorsal rays arise from dorsal.
- 30 (31). Spicules long and slender *Mirandaia* Travassos
- 31 (30). Spicules relatively short and stout *Dasypostrongylus* Travassos
- 32 (29). One dorsal ray arises with laterals *Heligmoskrjabinia* Freitas & Lent
- 33 (26). Other rays involved in asymmetry.
- 34 (37). Tips of spicules hooked.
- 35 (36). Externodorsal rays symmetrical, bursa short dorsally *Nippostrongylus* Lane
- 36 (35). Externodorsal rays asymmetrical, bursa long dorsally
..... *Austroheligmonema*, gen. nov.
- 37 (34). Tips of spicules simple.
- 38 (39). Ventral rays longer than any other *Mammolongistriata* Dubibin
- 39 (38). Ventral rays not longer than others.
- 40 (41). Both externodorsal rays arising from dorsal *Mastonema*, gen. nov.
- 41 (40). Externodorsal ray on left side arising with laterals *Oswaldonema* Travassos
- 42 (11). Bursal symmetrical or only slightly asymmetrical in size.
- 43 (48). Longitudinal cuticular crests absent.
- 44 (45). Spicules relatively long and simple *Viannaia* Travassos
- 45 (44). Spicules relatively stout and short.
- 46 (47). Gubernaculum present; female with acute tail and rudimentary posterior uterus
..... *Moennigia* Travassos
- 47 (46). Gubernaculum absent; female with truncated tail; monodelphous
..... *Pulchrostrongylus* Travassos
- 48 (43). Longitudinal crests present.
- 49 (60). Longitudinal crests incised at intervals, or otherwise varied.
- 50 (57). Alae present.
- 51 (52). Lateral alae bear asymmetrically placed hooks *Acanthostrongylus* Travassos

- 52(51). Cuticular hooks not present.
- 53(54). Longitudinal crests so interrupted as to appear imbricate in profile *Squamostrongylus* Travassos
- 54(53). Longitudinal crests so interrupted as to appear scalloped in profile.
- 55(56). Dorsal ray as long as longest laterals *Heligmostrongylus* Travassos
- 56(55). Dorsal ray not more than two-thirds length laterals *Heligmodendrium* Travassos
- 57(50). Alae absent.
- 58(59). Longitudinal crests so interrupted as to appear imbricate in profile *Trichotravassosia* Lent & Freitas
- 59(58). Longitudinal crests discontinuous forming numerous short narrow crests *Brevistriata* Travassos
- 60(49). Longitudinal crests simple.
- 61(62). Female with sac-like diverticulum from vagina *Avellaria* Freitas & Lent
- 62(61). Female without diverticulum from vagina.
- 63(64). Anus in female terminal *Philostrongylus* Wolfgang
- 64(63). Anus in female subterminal.
- 65(70). Spicules short, relatively stout, complex, or sinuous.
- 66(67). Spicules with enlarged extremities *Morganostrongylus* Fahmy
- 67(66). Spicules not enlarged distally.
- 68(60). Spicules sinuous; females monodelphous *Vianella* Travassos
- 69(68). Spicules straight; female with rudimentary posterior uterus *Pintonema* Travassos
- 70(65). Spicules elongate (more than 2.5 times prebursal body breadth) or if shorter [*Longistriata* (*Brevispiculoides*) spp.], simple in build.
- 71(74). Spicules bifid at tips.
- 72(73). Dorsal ray less than half laterals *Trifurcata* Schulz
- 73(72). Dorsal ray longer than laterals *Pudica* Travassos & Darriba
- 74(71). Spicules not bifid [except *Longistriata travassosi*, *L. norvegica*].
- 75(76). Dorsal ray shorter than externodorsals, bifurcate only at tip *Tricholinstowia* Travassos
- 76(75). Dorsal ray longer than externodorsal, or, if shorter, bifurcates before four-fifths of length.
- 77(78). Dorsal ray branches at or after three-quarters length; externodorsals very slender *Impalaia* Mönnig
- 78(77). Dorsal ray dividing proximal to three-quarters length, or if distal to this [*Longistriata zeta*, *L. cameroni*, *L. bathyergi*, *L. fortuita*, *L. musculi*, *L. schulzi*, *L. elpatievski*] then externodorsal ray not especially slender.
- 79(80). Dorsal ray very broad proximal to bifurcation *Evandroia* Travassos
- 80(79). Dorsal ray not especially broad.
- 81(82). Bursa much longer dorsally than laterally *Fuellebornema* Travassos & Darriba
- 82(81). Bursa longer laterally than dorsally (except *L. gracilis*, *L. moennigi*, *L. zeta*, *L. cameroni*, *L. spira*, *L. fortuita*, *L. travassosi*) *Longistriata* Schulz

Genus LONGISTRIATA Schulz

Longistriata Schulz, 1926, p. 24.

Heligmonella Mönnig, 1927, pp. 263-4.

Longistriata was proposed as a subgenus of *Viannaia* and was given generic rank by Travassos and Darriba. Travassos (1937, p. 321) comments that the type species, *Strongylus depressus* Dujardin, designated by Schulz, was unfortunately chosen, as it has never been properly described,* but that *L. wolgaensis* Schulz, described at the time the genus was erected, can be taken as an emergency type, at least for bursal characters.

*I understand from Dr. A. G. Chabaud (personal communication) that he has recently examined Dujardin's original drawings and he will be able to redescribe the species.

Heligmonella Mönnig as originally diagnosed is a synonym of *Longistriata*; Baylis (1928, p. 281) amended Mönnig's description but this does not alter the fact of synonymy. Mönnig's type, *H. spira*, is very similar to *L. wolgaensis* except in the presence of lateral alae and of much shorter spicules. *Heligmonella* has been accepted by some authors as a valid genus, differing from *Longistriata* in the presence of alae.

Among the many species attributed to *Longistriata* are a number in which alae are present, and the segregation of these into a subgenus or genus would seem no less useful than the segregation of those in which the bursa is asymmetrical or the spicules particularly short. Nevertheless, this would not be in accordance with the Rules, as it is not known if alae are present in the genotype *L. depressa* (Dujardin). Dujardin's description states only that there are four well-marked longitudinal crests on the body; these may include lateral alae.

Skrjabin, Shikhobalova, and Schulz (1954) recognize *Heligmonella*, even placing the genus in a different tribe from *Longistriata*, and attributing to it eight species, largely on the basis of the presence of lateral or ventral alae. Four of these are now considered to belong to *Longistriata*; of the others, one, *Heligmonella trifurcata* Baylis, is referred to *Heligmonina*; the other three, *H. streptocerca* Baylis, *H. jugatispiculum* Sadovskaya, and *H. vladimiri* Sadovskaya have symmetrical lateral alae and a bursa very distinctly asymmetrical in size only. It seems as logical to segregate these in a separate genus as to keep the species of the genera *Heligmonoides*, *Heligmonina*, and *Heligmospiroides* segregated as such, and, among so many species, such distinction simplifies identification. Accordingly a new genus, *Heligmobaylisia*, is proposed for them. A diagnosis is given under a separate head later in this work.

The bursa in *Longistriata* spp. is more or less symmetrical, but in some species which have been retained here it is slightly asymmetrical, though not so much as to indicate inclusion in any of the related genera; these species are *L. vexillata* (Hall), and *L. didas* Thomas. In some species, e.g. *L. vexillata*, *L. nematodiniiformis* Travassos, and *L. zeta* Travassos, the alae are developed dorsally and ventrally; the relationship of these to forms with lateral alae is not clear; the alae may be an exaggeration, natural or by fixing, of the condition noted by authors as "crests wider dorsally", e.g. *L. delta* Travassos.

A short-spiculed, non-alate species, *L. kurenzovi* Sadovskaya, doubtfully retained in the genus, shows a degree of bursal asymmetry close to that of *Heligmospiroides spira* Mönnig and of *Mirandaia ribeiroi* Travassos, but differs from the former in the absence of alae and from the latter in the disposition of the ventral rays.

Yeh (1958) erected the genus *Longistriatoides* to include two non-alate species of *Longistriata*, *L. codrus* Thomas and *L. trus* Thomas, which differ markedly from others of the genus in bursal characters; the dorsal ray is very long, and the bursa distinctly asymmetrical. The dorsal ray is long and the bursa slightly asymmetrical in *Longistriata cristata* Cameron (non *L. cristata* (Geddelst)) and in *L. zeta*; both of these species are alate. They are retained in *Longistriata*, but a new name must be given to *L. cristata* Cameron; *L. cameroni* is proposed.

Ortlepp (1939) proposed a subgenus, *Brevispiculoides*, to include species in which the spicules are short; this feature is of doubtful distinguishing value; Travassos (1937) proposed the limiting length being twice the body width, and Skrjabin, Shikhobalova, and Schulz (1954) as 2–3 times, the body width presumably being taken as that just in front of the bursa. In many species this factor can be arrived at only from the author's drawings, so that the range is not known, and in some species the spicules are only 3·5–4 times the breadth, rather too close for clear definition.

TABLE 2
MEASUREMENTS OF LONGISTRIATA MELOMYOS FROM THREE SPECIES OF RATS

Part Measured	<i>Melomys cervinipes</i>			<i>Melomys lutillus</i>	<i>Uromys caudimaculatus</i>		
	Range	No. of Specimens	Mean	Dimensions of 2 Specimens	Range	No. of Specimens	Mean
Male							
Length (mm)	3·4–5·3	12	4·2	4·1, 5·1	4·9–6·9	5	5·7
Oesophagus (μ)	280–370	12	316	260, 320	350–460	5	346
Anterior end to excretory pore (μ)	240–290	12	261	240, 270	300–380	5	326
Cephalic inflation (μ)	30–40	11	38	40, 40	40–50	4	46
Spicules (μ)	350–460	12	388	350, 500	600–680	5	648
Female							
Length (mm)	3·5–5·4	13	4·3	6·7, 5·7	5·5–7·3	9	6·2
Oesophagus (μ)	300–380	13	340	360, 330	390–450	9	412
Anterior end to excretory pore (μ)	240–340	11	288	300, 300	300–360	8	323
Cephalic inflation (μ)	35–40	7	42	40, 45	40–60	8	48·8
Tail (μ)	40–50	6	44	35, 50	40–45	3	43

The description of *L. cubaensis* Viguerras is not available to me. The remaining 55 species of the genus have been arranged in Figure 1 so as to indicate their main distinguishing characters. *L. depressa* has been placed in the centre of this diagram, not so much to indicate its position as genotype, but because, as mentioned above, its characters are not fully known.

LONGISTRIATA MELOMYOS, sp. nov.

(Figs. 2–8; Table 2)

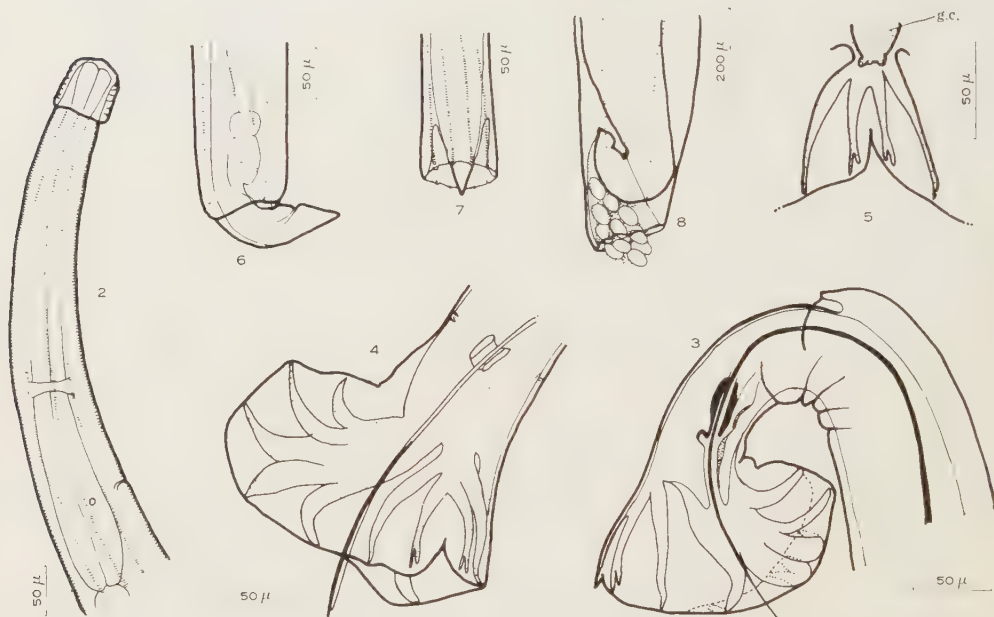
Host and localities.—*Melomys cervinipes*, Innisfail (type host and locality); *M. lutillus*, Innisfail, Whyanbeel, Miallo, Daintree; *Melomys* sp., Cairns; *Uromys caudimaculatus*, Innisfail.

The number of hosts infected with this species is indicated in Table 1. It is apparently the commonest trichostrongyle in *Melomys* spp. in this region, being

present not only in most host animals, but in larger numbers in each host than any other species. In *Uromys caudimaculatus* not more than three or four specimens were taken from each host, but these specimens were larger than those from *Melomys* spp. (see Table 2).

Cuticle transversely striated. Distinct but low longitudinal crests present, numbering 8 in anterior oesophageal region and about 16 over rest of body. In most specimens, males and females, cuticle more or less inflated towards posterior end of body. Cephalic cuticular inflation distinct and annulated.

Oesophagus widens slightly towards its base, surrounded by nerve ring just in front of two-thirds length; salient, rounded, cervical papillae at same level as opening of strongly cuticularized excretory duct, just in front of base of oesophagus.



Figs. 2-8.—*Longistriata melomyos*, sp. nov.: 2, anterior end; 3, bursa in usual position in fixed worm; 4, bursa, flattened; 5, dorsal and externodorsal rays, and genital cone (g.c.); 6, 7, and 8, posterior ends of three female worms.

Prebursal papillae present. Bursa symmetrical, 2-lobed, with dorsal cleft. Externodorsal rays arise from base of dorsal; latter bifid for nearly entire length, each stem ending in 2 short terminal branches. Arrangement of rays shown in Figure 4. Spicules long and slender, narrowly alate in distal half, weakly chitinized proximally. When dissected out, spicules seen to bear 2-3 longitudinal striae (? ridges). Spicule length between 5-7 times breadth of body just in front of bursa. Gubernaculum about 30 μ long, heart-shaped in dorsal view, with lateral extensions around spicules.

Tail of female short, conical, with rounded tip. Posterior end of body, at about level of vulva, bent ventrally at right angles to rest of body. Single uterus

and ovejector. Cuticle just in front of vulva more or less loose, in some overhanging the vulva (Fig. 6) and in others forming a short prepuce (Fig. 7). In some specimens a prepuce more strongly developed, completely surrounding posterior end of body (Fig. 8) and forming bell-shaped cavity filled with eggs and debris. Eggs are 55–65 μ by 30–40 μ .

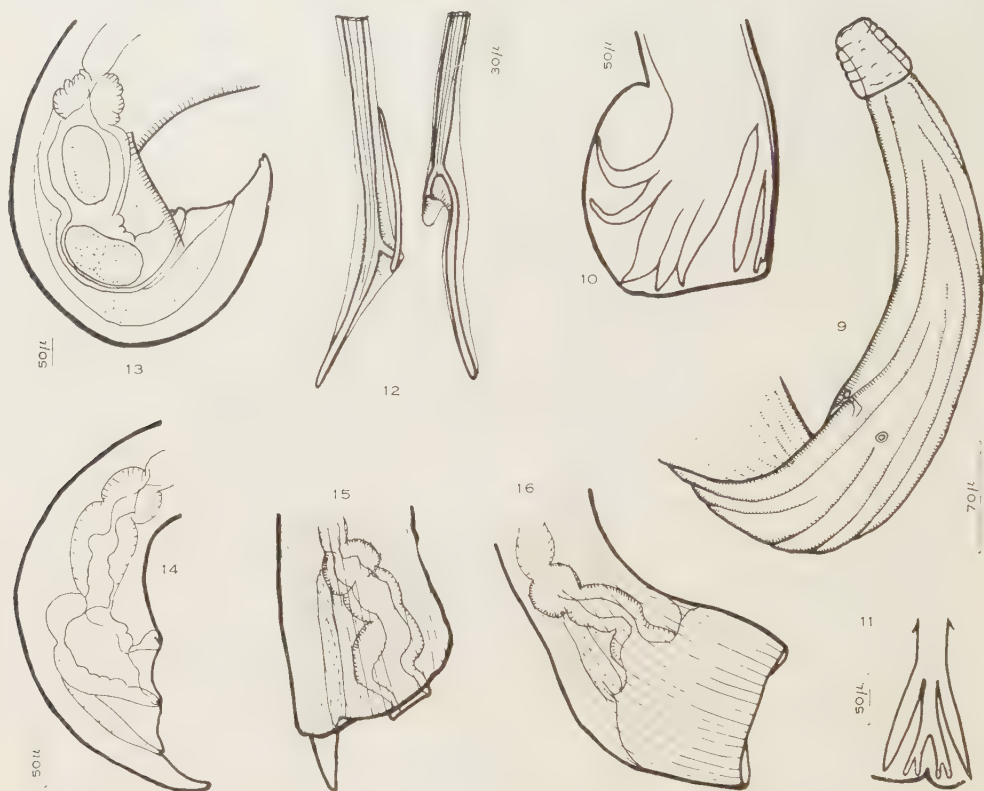
The species is very close to *L. wolgaense* Schulz (1926, p. 24) in the shape of the bursa and its rays. The cephalic swelling is of similar proportions and the cuticular crests and striae of the same type. The gubernaculum, however, has not the lateral distal processes, the spicules appear to be more delicate, and the worms

TABLE 3
MEASUREMENTS OF LONGISTRIATA UROMYOS, *L. BRACHYBURSA*, AND *L. POLYRHABDOTE*

Part Measured	<i>L. uromys</i>			<i>L. brachybursa</i>			<i>L. polyrhabdote</i>		
	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean
Male									
Length (mm)	4.3–7.2	20	5.3	2.9–3.7	13	3.2	2.9–3.3	5	3.0
Oesophagus (μ)	340–500	16	453	320–400	11	352	250–340	4	298
Anterior end to excretory pore (μ)	230–370	13	285	200–270	10	208	220–250	3	222
Cephalic inflation (μ)	45–65	9	53	35–40	11	37	40–50	4	45
Spicule (μ)	450–740	20	580	380–410	13	392	300–400	5	368
Spicule length/prebursal breadth	4–5	—	—	7.6–9.8	11	8.4	7.5–10	5	8.4
Female									
Length (mm)	3.8–7.3	17	5.3	3.9–4.4	8	4.2	3.5–4.5	10	3.9
Oesophagus (μ)	410–580	12	476	360–440	7	397	330–380	10	360
Anterior end to excretory pore (μ)	240–380	7	293	210–250	6	233	200–270	10	242
Cephalic inflation (μ)	45–70	8	58	37–40	6	39	45–55	10	49
Tail (μ)	60–70	3	65	35–50	8	40			

are distinctly larger. *L. wolgaense* was described from a single male specimen from a Russian rat. Yamaguti (1954, p. 119) has recorded it from three Japanese rats, describing but not figuring both sexes. His description differs from that of Schulz in the position of the excretory pore, the point of origin of the externodorsal ray, and the shape of the gubernaculum. The females described by Yamaguti are very similar to those of the Australian species. *L. wolgaense* has also been recorded from *Clethrionomys glareolus* from the Shetland Is. (Thomas 1953, p. 148). Thomas does not state the position of nerve ring or excretory pore, or the length of the oesophagus; he described the cephalic inflation as "small or absent"; gubernacular processes are not described or figured; the ventroventral ray is much shorter, and the externodorsal rays of different proportions to the

dorsal ray, than figured by Schulz; the female differs from that described by Yamaguti in the egg shape and the flexure of the tail region. In view of these differences in interpretation of the species, the Australian specimens are considered as a new species.



Figs. 9-16.—*Longistriata uromyos*, sp. nov.: 9, anterior end; 10, bursa, lateral view; 11, dorsal and externodorsal rays; 12, spicules, dissected out of body; 13, 14, 15, and 16, stages in the development of the posterior end of female. All figures to same scale.

LONGISTRIATA UROMYOS, sp. nov.

(Figs. 9-16; Table 3)

Type host and locality.—*Uromys caudimaculatus*, Innisfail.

Relatively large worms; body coiled into a spiral. Cuticle with marked transverse striae and low longitudinal crests, about 8 crests behind cephalic inflation, and posterior to this more arise from lateral lines and pass back obliquely; at widest part of body about 40 crests in male. Crests easier to see, especially posteriorly, on detached cuticle. Cephalic inflation with annuli.

Oesophagus slightly wider posteriorly. Excretory pore and cervical papillae at same level, between one-half and two-thirds length of oesophagus from head.

Bursa symmetrical, bilobed, with slight dorsal incision. Dorsal ray long, dividing into 2 at about three-quarters its length, each branch bifid at tip.

Externodorsal rays arise from mid-length of dorsal and lie close to it. Arrangement of lateral and ventral rays seen in Figure 10. Spicules stout, strongly chitinized and alate, each with dorsal heel-like projection about $60\ \mu$ from distal end, supporting short fan-like alae. This projection apparently folded against shaft of spicule when inside body, and springing out when spicule protruded or dissected out. When spicule dissected out, apparent gubernaculum seen to be formed of 2 parts, a cuticularized ring remaining in wall of spicule tube, and a long, slender, dorsal plate coming off loosely attached to one spicule; this plate is not normally extruded with spicules. Spicules with longitudinal striae. Spicule length about 4-5 times the prebursal body breadth.

Relationship of female to male is established by the similarity of body form, structure of anterior end, and the numerous longitudinal crests (up to 48) as well as by its being, as is the male, the most numerous species in the host animals. The posterior end of the female varies in shape, apparently with age, or state of development, of the worm. The tail is a long cone without terminal spike. Body widens abruptly in front of anus and in most specimens posterior end is curved ventrally. In several collections development of tail region appears to have progressed further. The cuticle around the vulva is thickened, and the pre-anal body widens greatly, so that flexure of tail is less marked (Figs. 14, 15); further development is the loosening and inflation of the cuticle in this region and the formation of a bell-like prepuce overhanging the posterior end (Fig. 16); the tail becomes more or less flattened against the dorsal wall of the bell. In early stages, there is a vestibule leading in from the vulva, and this in later stages is much shorter, whether by partial evagination or by stretching is not clear. Eggs are $70\ \mu$ by $35-40\ \mu$.

The species is distinguished from *L. melomyos*, which is present in many of the same host animals, by the characters of bursa and spicules and by the shape of the female tail, the type of expansion at the posterior end of the older female, as well as by the position of the excretory pore and more numerous cuticular crests.

In the form of the bursa it closely resembles *L. capensis* Ortlepp but the ventral rays and the shape of the spicules are different; the tip of the spicules resembles those of *L. travassosi* Lent & Freitas but the bursal rays are different.

LONGISTRIATA BRACHYBURSA, sp. nov.

(Figs. 17-20; Table 3)

Hosts and localities.—*Melomys cervinipes*, Innisfail (type host and locality); *M. lutillus*, Innisfail.

Small worms, usually whole body coiled in a close spiral. Cuticle with numerous marked transverse and longitudinal striae as well as longitudinal crests about 8 behind cephalic inflation and up to 16 further back on body.

Excretory pore and short slender cervical papillae lie at same level, a little in front of two-thirds oesophageal length; nerve ring behind mid-oesophagus.

Posterior end of female flexed sharply back on itself. Tail conical, relatively long, pointed at the tip. Vagina with typical kink before joining ovejector. Eggs $55-60\ \mu$ by $30-40\ \mu$. No specimen was seen with any cuticular fold in the tail region.

Bursa symmetrical with long lateral lobes and short dorsal lobe with median cleft. In Figure 18, depicting the most common position of the bursa in fixed specimens, the lateral lobes appear to be of unequal size; this is because one is



Figs. 17-20.—*Longistriata brachybursa*, sp. nov.: 17, oesophageal region; 18, bursa, in usual position; 19, bursa, flattened; 20, posterior end of female. Figs. 21-24.—*Longistriata polyrhadote*, sp. nov.: 21, oesophageal region, 22 and 23, bursa; 24, posterior end of female.

furled around the other, but they are of equal size, or almost so. Arrangement of bursal rays shown in Figure 19. Spicules long, expanding near tips into 2 alate branches; gutter-shaped gubernaculum 25μ long present. This species is characterized by the short dorsal lobe of the bursa and expanded tips of the spicules. In the form of the bursa and its rays it most resembles *L. depressa* (though not as redescribed by Thomas 1953, p. 152), and *L. delta*, but in both of these species the spicules are simple.

LONGISTRIATA POLYRHABDOTE, sp. nov.

(Figs. 21–24; Table 3)

Type host and locality.—*Rattus assimilis*, Mt. Glorious.

Small worms, loosely coiled in 1 or 2 turns. Head cuticle inflated and distinctly annulated. Longitudinal crests small and very numerous, up to 40 in widest part of body. Oesophagus slender, surrounded by nerve ring at about mid-length. Excretory pore at level of three-quarters length of oesophagus, at same level as cervical papilla.

Bursa of male symmetrical, bilobed, with deep dorsal cleft. Arrangement of rays shown in Figures 22, 23. Genital cone elongate, with cloacal opening at its apex. Spicules lightly chitinated with simple tips, their length about 7·7–10 times prebursal body breadth. Gubernaculum 20 μ long, not strongly developed.

Posterior end of female tightly twisted into 1½ or 2 coils commencing a little in front of the vulva, so that exact measurements are impossible. Tail ends in a narrow digitiform projection, pointed at the extremity (Fig. 24). Eggs 65–70 μ by 30–35 μ .

The species occurred in only one host specimen; in this another species, *Austroheligmonema typicum*, was also present in about equal numbers. The females described above were differentiated from those *A. typicum* by the form of the tail ending, and were associated with the male described above by the type of cuticular striation. The species is distinguished from most others of the genus by the twisted female tail. In *Heligmobaylisia streptocerca* (Baylis) the tail of the female is twisted but the bursa is different. A similarly twisted tail is figured by Cameron (1939, p. 26, fig. 38) for "*Heligmosominae* sp. inq." from a pigmy anteater in Trinidad.

Genus HELIGMONOIDES Baylis

Heligmonoides Baylis, 1928, p. 294.Type species *Heligmonoides murina* Baylis, 1928.

The genus *Heligmonoides* was first described by Baylis as being close to *Heligmonella* but with the left lobe of the bursa much larger than the right; alae are not specified, except by analogy with *Heligmonella*, of which Baylis states (in an amendment of the generic diagnosis, 1928, p. 291) that alae may be present or absent, and one may be larger than the other. In the description of the type (and only) species described by Baylis, *Heligmonoides murina*, alae are not mentioned or figured. However, later authors (Khalil 1932, p. 444; Freitas, Lent, and Almeida 1937; Travassos 1937, p. 357; Ortlepp 1939, p. 92; Skrjabin, Shikhobalova, and Schulz 1954, p. 204) have interpreted the genus as characterized by a much-enlarged left lateral ala. Chandler (1932, pp. 28, 30) does not make this mistake. Freitas, Lent, and Almeida in describing their species, *H. mazzai*, do not mention a lateral ala in their description, and in discussion say:

"Em nossos exemplaires nao podemos garantir a existencia de uma aza lateral esquerda, devido a sua fixacao precaria, dando origem a garnde inflacao da cuticla."

It seems that this genus should be interpreted as including species in which there is a bursa with the left lobe larger than the right, and in which lateral alae

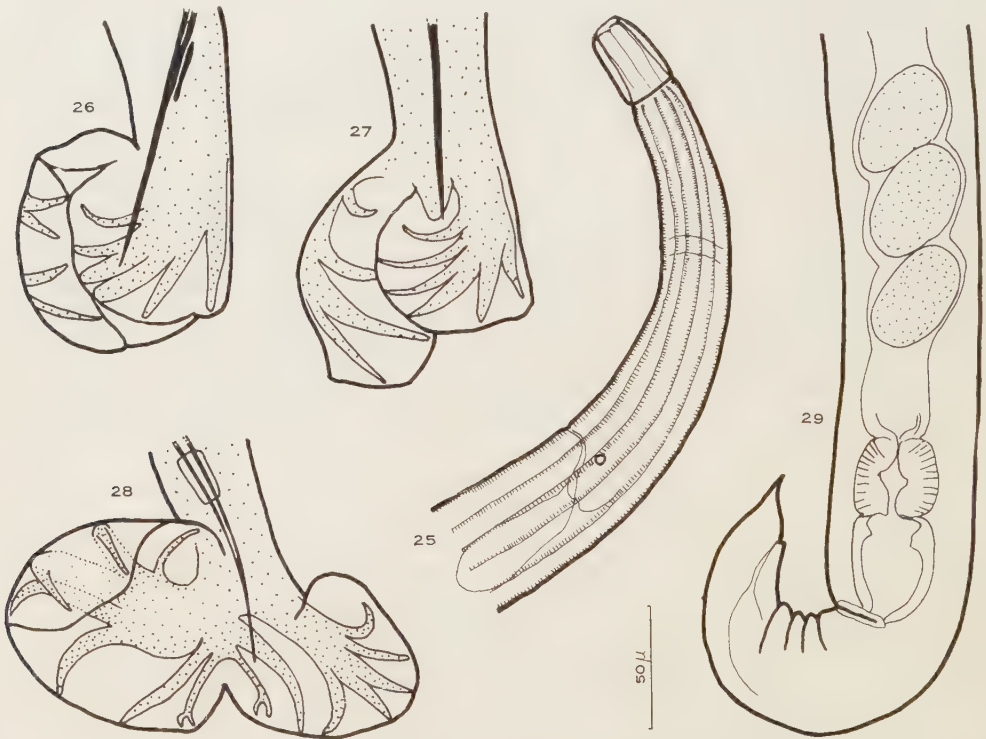
are absent or unobtrusive. *H. murina* and *H. mazzai* are therefore rightly attributed to it, but *H. vogeli* (Khalil) and *H. stellenboschius* Ortlepp in which one ala is greatly developed belong more properly in the genus *Heligmonina*.

Two new species are described below.

HELIGMONOIDES MACKERRASAE, sp. nov.

(Figs. 25–29; Table 4)

Hosts and localities.—*Melomys cervinipes*, Innisfail (type host and locality); *M. lutillus*, Innisfail, Whyanbeel, and Daintree; *Melomys* sp., Cairns; *Uromys caudimaculatus*, Innisfail.



Figs. 25–29.—*Heligmonoides mackerrasae*, sp. nov.: 25, anterior end of female; 26, 27, and 28, views of bursa; 29, posterior end of female. All figures to same scale.

Small worms from stomach, duodenum, and, most commonly, ileum. Most of fixed specimens in flat coil with posterior end projecting tangentially. Annulated cephalic cuticle present. Cuticle of rest of body transversely striated, with 10–12 longitudinal crests anteriorly, up to 16 further back. Cuticle on ventral body very slightly inflated, especially anteriorly, and transverse striae on ventral crests have block-like appearance.

Oesophagus slender with slight kink just in front of mid-length where it is surrounded by nerve ring, and behind this widening slightly. Very distinct

excretory pore, and rounded insignificant cervical papillae at about same level, just in front of posterior end of oesophagus.

Bursa asymmetrical, right lobe larger than left. Dorsal lobe not separated from laterals, deep dorsal cleft present. In unflattened fixed specimens lateral lobes folded inwards, one over the other. Right and left rays of similar form, those of right side stouter and longer. Arrangement of rays shown in Figures 27 and 28. Spicules slender, not strongly chitinized, and with simple points apparently joined. Gubernaculum lightly chitinized, about $25\ \mu$ long. Spicule length is about 9.5–10 times prebursal body width.

TABLE 4
MEASUREMENTS OF *HELIGMONOIDES MACKERRASAE* AND *H. EMANUELAE*
All specimens measured were from the type host of the species

Part Measured	<i>H. mackerrasae</i>			<i>H. emanuelae</i>		
	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean
Male						
Length (mm)	2.2–2.7	11	2.4	2.2–2.6	10	2.3
Oesophagus (μ)	190–230	9	210	240–270	10	254
Anterior end to excretory pore (μ)	170–215	8	191	190–220	9	202
Cephalic inflation (μ)	30–45	8	32	50–60	10	52
Spicules (μ)	380–410	9	388	250–330	10	297
Female						
Length (mm)	2.5–3.2	10	2.9	2.1–3.1	10	2.6
Oesophagus (μ)	220–260	10	236	270–290	9	280
Anterior end to excretory pore (μ)	180–215	10	200	200–222	9	210
Cephalic inflation (μ)	30–37	10	33	50–60	10	55
Tail (μ)	—	—	—	40–50	10	45

Posterior end of female bent ventrally so much that tail directed anteriorly. Tail short, conical, ending in narrow elongated point. Eggs $55\text{--}58\ \mu$ by $30\text{--}32\ \mu$.

The species differs from *H. mazzai* in the origin of the externodorsal ray from the base of the dorsal ray, and in the shape of the tail of the female.

HELIGMONOIDES EMANUELAE, sp. nov.

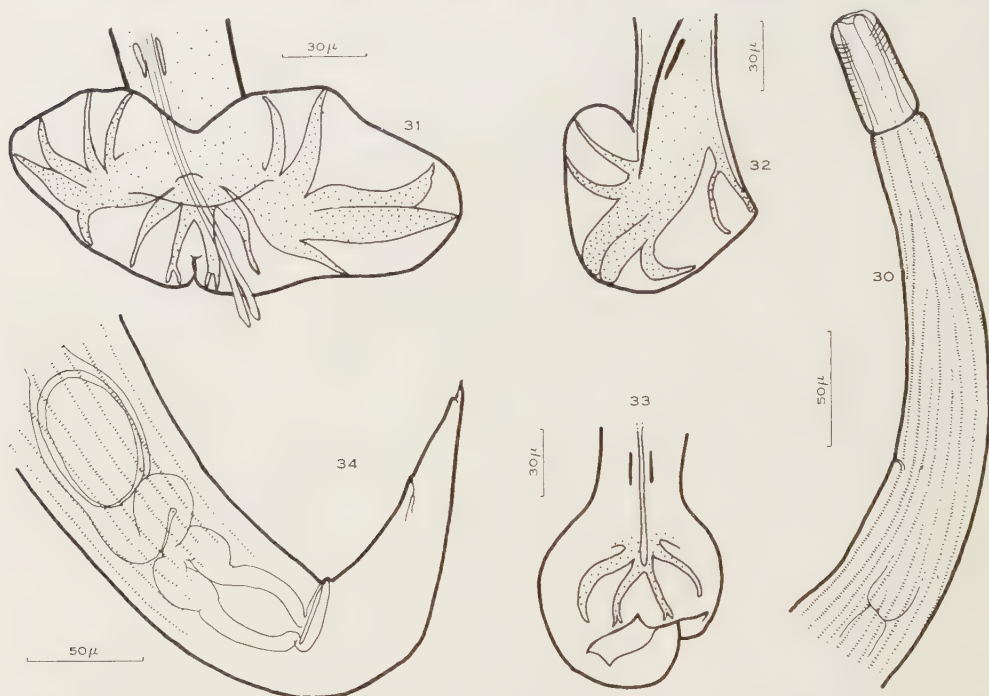
(Figs. 30–34; Table 4)

Hosts and localities.—*Rattus conatus*, Innisfail (type host and locality); *R. assimilis*, Innisfail and Miallo.

Small worms from small intestine, fixed specimens in 1 or 2 coils. Cephalic inflation relatively long, and distinctly annulated. Cuticle with very distinct longitudinal striae, transverse striae not marked except on longitudinal crests, which number up to 20 on middle part of body. Digitiform cervical papillae present, at same level as excretory pore, at about three-quarters length of oesophagus. Nerve ring at about mid-oesophagus.

Posterior end of female flexed at right angles just behind vulva and body behind this tapers in long cone to bluntly pointed tip of tail, with 2 relatively large ventrolateral subterminal processes. Vulva about $65\text{--}80\ \mu$ in front of anus, about 1.5 times tail length; ovejector short and adjacent part of uterus always with short loop. Eggs relatively large, $60\text{--}80\ \mu$ by $30\text{--}40\ \mu$.

Bursa asymmetrical, left lobe longer than right; dorsal cleft present but no dorsal lobe. Rays of both sides of similar shape, those of left side larger. Dorsal



Figs. 30–34.—*Heligmonoides emanuelae*, sp. nov.: 30, anterior end of female; 31, bursa opened out; 32 and 33, lateral and dorsal views of bursa; 34, posterior end of female.

and externodorsal rays symmetrical; arrangement of rays shown in Figures 31 and 33. Spicules long and slender, tips widened and alate; spicule length 7.0–8.2 times prebursal body width.

The species differs from *H. mackerrasae* from *Melomys* spp. and *Uromys* sp. in the characters of cuticle, female tail, bursa (in which the opposite side is enlarged and externodorsal rays a different size compared with the dorsal), and in the relative spicule length.

Genus HELIGMONINA Baylis

Heligmonina Baylis, 1928, pp. 280–304.

Type species *Heligmonina praomyos* Baylis, 1928.

Heligmonina was defined by Baylis as having the left ala enormously developed, a bursa with asymmetrical lateral lobes, the left much larger than the right and with longer rays, and with the dorsal ray symmetrical or not. In the type

species, *H. praomyos*, the dorsal ray is asymmetrical, in *H. magna* Baylis it is symmetrical. The only other species included by Baylis, *H. cricetomyos*, in which the bursal asymmetry is more extensive, has been made the type of another genus, *Trichobaylisia*. Ortlepp (1939, p. 93) proposed a subgenus *Paraheligionina* for *H. magna*, noting the symmetry of the dorsal ray. *H. trifurcata* (Baylis), syn. *Heligionella trifurcata*, *Heligionina vogeli* Khalil, and *H. stellenboschius* (Ortlepp), syn. *Heligionoides stellenboschius*, should also belong in this subgenus. The exclusion of the two last-named from *Heligionoides* is discussed above, under that genus.

Genus HELIGMOBAYLISIA, gen. nov.

Heligionella Mönnig, 1927, pp. 263-4, pro parte.

Type species *Heligionobaylisia streptocerca* (Baylis), syn. *Heligionella streptocerca*; other species: *Heligionobaylisia jugatispiculum* (Sadovskaya), syn. *Heligionella jugatispiculum*, and *Heligionobaylisia vladimiri* (Sadovskaya), syn. *Heligionella vladimiri*.

The constitution of this genus was discussed above, under *Longistriata*. Its diagnosis is as follows: With inflated cephalic cuticle; rest of cuticle with longitudinal crests two of which form symmetrical lateral alae. Monodelphic vulva near anus. Bursal lobes asymmetrical in size, rays similar in form; ventral rays divergent, antero- and mediolaterals together, posterolateral divergent, externo-dorsals arising dorsally; dorsal bifurcating tips divided or not; spicules relatively long and slender. Parasites of rodents.

Genus NIPPOSTRONGYLUS Lane

NIPPOSTRONGYLUS BRASILIENSIS (Travassos) Travassos & Darriba

(Figs. 35-40; Table 5)

Heligmosomum brasiliense Travassos, 1914, p. 323.

Heligmosomum muris Yokogawa, 1920, p. 29.

Nippostrongylus muris (Yokogawa) Lane, 1922, p. 360.

Nippostrongylus brasiliensis (Travassos) Travassos and Darriba, 1929, p. 432.

Hosts and localities.—*Rattus rattus*, Innisfail and Bartle Frère, *R. norvegicus*, *R. assimilis*, and *R. conatus*, Innisfail.

Other host and locality records for this species under its various synonyms are given in the following tabulation:

H. brasiliense

R. norvegicus (*Mus decumanus*), Brazil (Travassos 1914), type host and locality

R. (Epimys) norvegicus, Sydney and Brisbane (Johnston 1918a)

R. (E.) rattus, Brisbane (Johnston 1918b)

R. (E.) norvegicus, England (Dudgeon 1923)

R. (E.) norvegicus, Townsville, Qld. (uncertain diagnosis of parasite species) (Fielding 1928)

H. muris

R. (E.) norvegicus, Baltimore (Yokogawa 1920, 1922)

R. (Mus) rattus, *R. (M.) norvegicus*, Canton (Wu 1930)

TABLE 5
MEASUREMENTS OF NIPPOSTRONGYLUS BRASILIENSIS FROM DIFFERENT HOST SPECIES

Part Measured	<i>R. rattus</i>			<i>R. norvegicus</i>			<i>R. assimilis</i>			<i>R. conatus</i>		
	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean
Male												
Length (mm)	3.6-4.1	5	3.9	2.6-3.9	5	3.3	3.3-3.8	3	3.5	2.5-3.4	7	3.0
Oesophagus (μ)	310-330	4	316	310-380	4	342	260-360	3	300	310-390	7	349
Anterior end to excretory pore (μ)	240-280	5	262	220-260	5	258	220-250	3	240	240-270	7	259
Cephalic inflation (μ)	70	5	70	50-70	5	61	60-65	3	63	60-70	7	61
Spicules (μ)	530-580	5	560	440-570	5	518	500-560	3	533	470-500	6	458
Spicule length/prebursal breadth	7.6-9.5	4	8.8	7.6-8.8	4	8.2	9.3-10	3	9.7	8.5-9.0	4	8.7
Female												
Length (mm)	4.2-5.7	5	5.0	4.1-4.6	5	4.24	3.3, 3.7	2	3.5	2.7-3.5	5	3.0
Oesophagus (μ)	310-340	4	328	300-360	5	330	310, 290	2	300	300-360	5	336
Anterior end to excretory pore (μ)	240-290	4	263	250-270	5	258	300, 270	2	285	170-270	5	212
Cephalic inflation (μ)	65-75	3	70	60-70	5	67	60, 60	2	60	50-60	5	58
Tail (μ)	30-45	4	40	30-40	3	35	30, 35	2	33	30-40	5	34

N. muris

"Samoa rat", Samoa (Lane 1922)

R. (Mus) norvegicus, Philippine Is. (Tubangui 1931)

R. (Mus) rattus, Canton (Chen 1933)

Mus musculus and *R. (E.) norvegicus*, Baltimore (Porter 1934, 1935a, 1935b)

Peromyscus maniculatus, Baltimore (experimental infection not completely successful) (Porter 1934)

R. (E.) norvegicus, Peiping (Ko 1938)

N. brasiliensis

R. rattus alexandrinus, Kyoto, Japan (Yamaguti 1941)

R. norvegicus or *R. rattus* or both, Costa Rica (Vives and Zeledon 1957)

R. conatus, Innisfail (Mackerras 1958)

It is noted by Johnston (1918a, p. 56) that the parasite is apparently rare in Sydney and Brisbane. He states "It was met with on only two occasions in Sydney though some hundreds of brown rats were dissected". Fielding (1928, p. 126), in the course of an investigation into the incidence of rats carrying plague, examined 1779 rats and mice* from the Townsville area, and found only one infection with a trichostrongyle worm, which was suspected to belong to this species, but was not positively identified. *N. brasiliensis* appears to be more common than this in the Innisfail region; it will be noted from Table 1 that the species is very common in *R. rattus*, less so in other *Rattus* spp., and not present in any collection from *Melomys* spp., *Uromys* sp., or *Hydromys* sp.

N. brasiliensis has recently been used as an experimental animal by L. E. Symons and R. Simmonds in Sydney. The worms used in this research are from a strain imported from Baltimore.

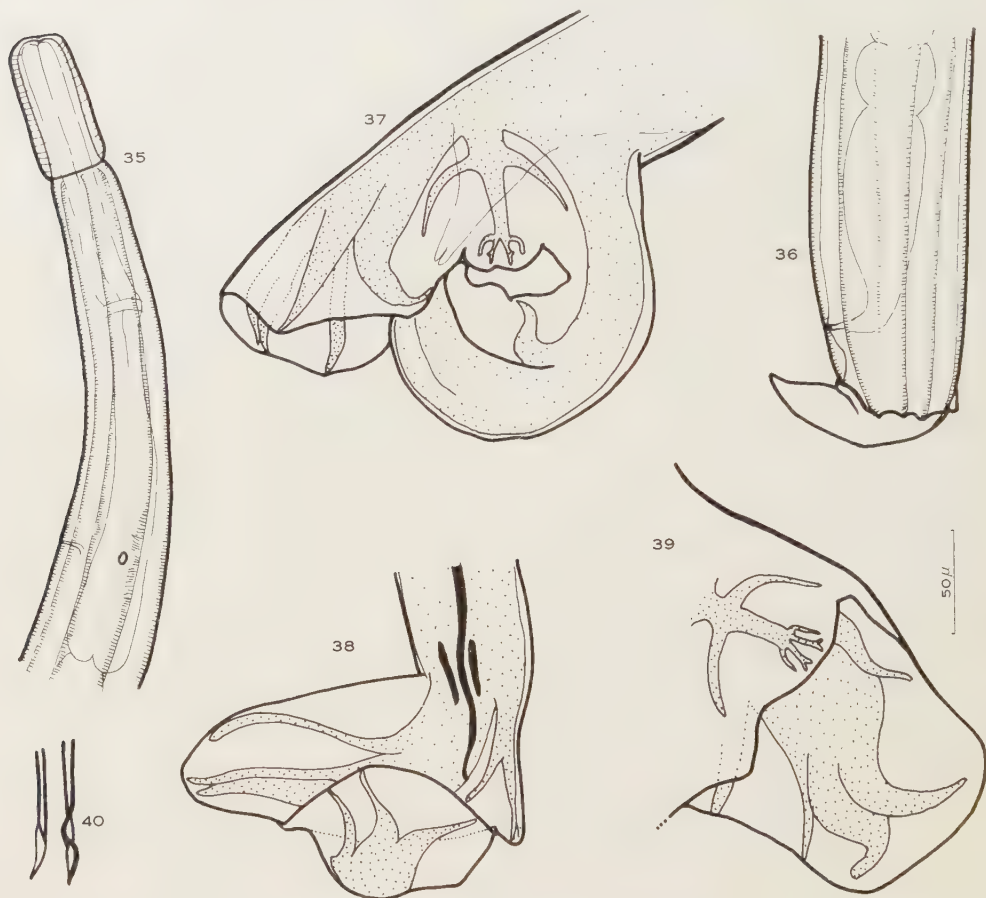
Although the species has been recorded from England, Japan, China, and the Pacific area, as well as America, where it has been frequently used as an experimental animal, full descriptions are rare. The specimens from Queensland have been studied from different hosts, and the measurements compared in Table 5. As some of the earlier accounts do not agree on some points, the following observations are offered:

- (1) Cuticle raised into distinct longitudinal crests of about equal size: about 10 anteriorly and posteriorly and about 16 in the wider parts of the body.
- (2) Cuticular cephalic inflation is long, its length rather more than twice its diameter.
- (3) Cervical papillae, stated to be absent in this species (Tubangui, Yokogawa) or not mentioned (Travassos, Johnston) are small but distinct in all Australian specimens, including those of Johnston,† now re-examined, lying at level of excretory pore; nerve ring not distinct, a little in front of mid-oesophagus, at position of slight kink noted by Yamaguti (1941, p. 415).
- (4) Bursa very asymmetrical, right lobe longer than left; dorsal lobe short but distinct.

* The rodents examined belonged to the species *Rattus rattus*, *R. rattus alexandrinus*, *R. norvegicus*, *Hydromys chrysogaster*, and *Mus musculus*.

† Johnston's specimens are in the Helminthological Collection (H.C. 2487), Zoology Department, University of Adelaide.

- (5) Rays in left lobe quite different in form from those of right, but dorsal and externodorsal rays symmetrical. Arrangement of rays, shown in Figures 37, 38, and 39, corresponds with descriptions and figures given by Johnston, Tubangui, Lane, and Ko, but not with those of Yokogawa or Travassos. In keys to genera of Heligmosomatidae, *Nippostrongylus*



Figs. 35-40.—*Nippostrongylus brasiliensis* (Travassos): 35, anterior end of female; 36, posterior end of female; 37 and 38, views of bursa, with lobes folded in the two positions most commonly seen in fixed specimens; 39, dorsal and right lobes of flattened bursa; 40, tips of spicules. All figures to same scale.

is included (Travassos, Chandler, Skrjabin *et al.*) among those in which "dorsal ray short, not reaching bursal edge"; actually the dorsal ray reaches the edge of the short dorsal lobe of the bursa, and in this respect differs not at all from some *Longistriata* spp., e.g. *L. brachybursa*, *L. convoluta*, *L. norwegica*.

- (6) Spicule length about 7-10 times prebursal body width. Spicule tips slightly curved and alate, that of the stouter spicule more strongly so.

- (7) Gubernaculum, about 30–40 μ long, and telamon, about 70 μ long, both present.
- (8) Tail of female short, conical, without sharp tip or spine, and almost always curved ventrad at right angles to body; small ventral projection of cuticle overlies vulva, in most cases extending right round body, and in a few cases projecting to form well developed prepuce covering tail. Eggs 50–70 μ by 30–40 μ .

Genus AUSTROHELIGMONEMA, gen. nov.

Type species *Austroheligmonema typicum*, sp. nov.

Diagnosis.—Cephalic inflation and longitudinal cuticular crests present, buccal cavity and teeth absent. Right side of bursa much larger than left, and ventral, lateral, and externodorsal rays asymmetrical in form and size. On right side ventral rays separate from each other and from laterals for most of their length, antero- and mediolaterals, the longest rays, diverge only at tips, posterolateral short; on left side, two ventrals and anterolateral parallel, mediolateral divergent from them, all about same length; posterolateral ray long, divergent for most of its length; dorsal ray arises from right posterolateral, externodorsals of different size leave dorsal ray asymmetrically; dorsal ray bifurcates near distal end and branches divide again more or less symmetrically. Spicules simple, elongate, tips hooked; gubernaculum present. Posterior end of female bent ventrad, tail conical; body wall around vulva swollen. Parasites of rodents.

This new genus is proposed for two very similar species, *A. typicum* from southern Queensland and *A. magnum* from northern Queensland. In the form of the bursa the genus resembles *Nippostrongylus*, *Oswaldonema*, and *Heligmoskrjabinia*. The asymmetry is greater than in *Nippostrongylus* and less so than in the other two genera. The long gap between the right externodorsal and right posterolateral rays gives the bursa a different basic structure from that of species of the other three genera. The tips of the spicules are unlike those in *Oswaldonema* or *Heligmoskrjabinia*. The dorsal ray and lobe are larger, and of different form, than in *Nippostrongylus*. In *Trichobaylisia*, marked asymmetry, especially of the externodorsal rays, is also present, but to a lesser extent, and in this genus lateral alae are present.

AUSTROHELIGMONEMA TYPICUM, sp. nov.

(Figs. 41–45; Table 6)

Type host and localities.—*Rattus assimilis*, Mt. Nebo, Mt. Glorious.

Small slight worms, body usually rolled into 2 or 3 coils. Cephalic inflation present, 50–60 μ long, cuticle with well-marked longitudinal crests, about 10 behind cephalic inflation, up to 16 further back. Cervical papillae distinct but small, at level of excretory pore, three-quarters to seven-eighths of length of oesophagus from its base. Oesophagus widening gradually towards base, surrounded by nerve ring shortly behind mid-length.

Bursa and rays quite asymmetrical, left side larger; hardly any separation between lobes, but between dorsal ray and right lateral rays bursa is shortest and in this part bursal wall is thickened by what appears to be a deposit of finely granular material, making it more opaque than the rest of the bursa. This is shown in Figures 42 and 43 as a dotted area. The arrangement of the rays is shown in Figures 42 and 43. Spicules long and slender, enlarged at proximal ends, tips apparently joined and forming a small hook, subtending short narrow alae. Gubernaculum about 25–35 μ long, curved laterally around spicules. Genital cone very distinct, long and slender, truncate distally.

TABLE 6
MEASUREMENTS OF AUSTROHELIGMONEMA TYPICUM, A. MAGNUM, AND MASTONEMA MELOMYOS
All measurements given of specimens from type host of the species

Part Measured	<i>A. typicum</i>			<i>A. magnum</i>			<i>M. melomyos</i>		
	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean	Range	No. of Specimens	Mean
Male									
Length (mm)	2.3–3.1	16	2.8	3.2–4.1	10	3.6	7.6–9.8	10	8.2
Oesophagus (μ)	310–340	16	248	310–360	10	340	280–330	10	311
Anterior end to excretory pore (μ)	230–280	16	248	250–300	9	272	370–440	7	413
Cephalic inflation (μ)	50–60	16	56.3	60–70	10	64	60–70	8	66
Spicules (μ)	270–330	16	308	480–580	10	539	570–800	9	704
Female									
Length (mm)	3.0–4.0	11	3.4	3.7–4.4	10	4.1	14.0–18.1	10	15.5
Oesophagus (μ)	310–410	11	370	330–490	10	366	350–460	10	406
Anterior end to excretory pore (μ)	180–270	11	240	260–310	10	277	420–580	9	493
Cephalic inflation (μ)	45–60	11	51	65–70	5	67	70–80	4	74
Tail (μ)	25–30	4	29	30–35	3	32	65–70	10	69

Posterior end of female flexed between anus and vulva, so that tail at right angles to body. Cuticle in prevulvar region slightly inflated. Tail short, bluntly conical. Vulva on ventral body wall with distinctly chitinized lips. Eggs 65–70 μ by 28–30 μ .

AUSTROHELIGMONEMA MAGNUM, sp. nov.

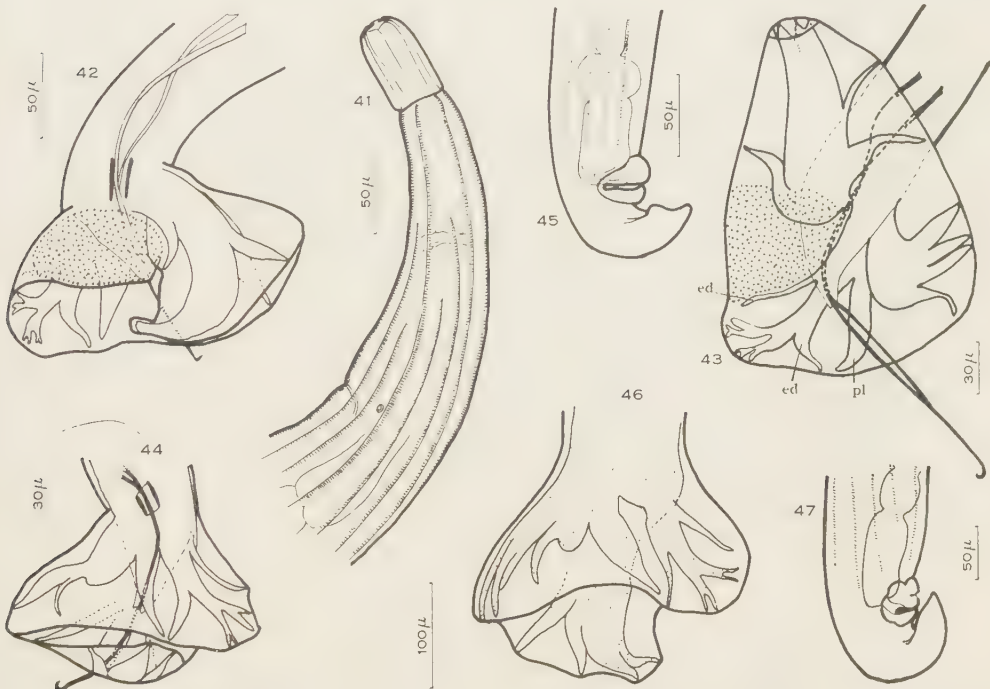
(Figs. 46, 47; Table 6)

Hosts and localities.—*Rattus assimilis*, Innisfail, Miallo, and Mossman; *R. rattus*, *R. conatus*, *R. norvegicus*, Innisfail; *Melomys cervinipes*, Innisfail.

Coiled worms from small intestine; body loosely coiled; striated cephalic inflation present. Twelve to 14 longitudinal ridges present on widest part of body, fewer anteriorly. Cervical papillae and excretory pore at same level, about three-

quarters length of oesophagus from anterior end. Nerve ring at about end of anterior third of oesophagus.

Bursa and rays asymmetrical, arranged as shown in Figure 46. Rays very similar in arrangement to those of *A. typicum* but whole bursa distinctly larger. Wide space between dorsal ray and right lateral rays as in *A. typicum*, but without mass of granular material. Spicules long and slender, strongly chitinized, tips unequal, the more slender ending in slight curve fitting into stronger curve of tip of stouter.



Figs. 41–45.—*Austroheligmonema typicum*, gen. et sp. nov.: 41, oesophageal region; 42, 43, and 44, views of bursa; 45, posterior end of female. Figs. 46 and 47.—*Austroheligmonema magna*, gen. et sp. nov.: 46, bursa; 47, posterior end of female; *ed*, externodorsal ray; *pl*, posterolateral ray.

Tail of female conical with simple tip. Body flexed between vulva and anus so that tail directed anteriorly. Strongly developed perivulvar cuticular thickening. Eggs 50–55 μ by 30–32 μ .

The species is distinguished from *A. typicum* by the shape of the spicules, absence of granular mass in bursa, greater flexure of tail, and fewer and more marked ridges, as well as by the greater size.

Genus MASTONEMA, gen. nov.

Type species *Mastonema melomyos*, sp. nov.

Diagnosis.—Cephalic cuticle inflated and annulated; rest of cuticle with transverse and longitudinal striae and longitudinal crests from postoesophageal

region to some little distance in front of vulva. Excretory pore postoesophageal; bursa asymmetrical, right side the larger; ventral rays and ventro- and mediolateral rays differing mainly in size, posterolaterals quite different, left arising separately and lying beside dorsal, right arising with other laterals and diverging after short distance; externodorsals of unequal thickness, leaving dorsal ray at about one-quarter its length, shorter than dorsal and lying close beside it; dorsal ray bifurcates at about three-quarters length, further branching not clear. Spicules long and slender, tips simple. Gubernaculum not strongly developed. Posterior end of female strongly recurved, tail conical; vulva short in front of anus. Parasitic in mammary gland of rodents.

Two trichostrongyles, both from Russia, have been described from the mammary gland of their host, *Mammanidula asperocutis* Sadovskaya from a shrew, and *Mammolongistriata mammovitae* W. Dubinin from a rodent. The only descriptions of these available to me are those given by Skrjabin, Shikhobalova, and Schulz (1954, pp. 263 and 292 respectively). In this work, *Mammanidula* is placed in the subfamily Viannaiinae, as longitudinal cuticular crests are absent, although the spicules are long and thin. *Mammolongistriata* is in the same subfamily although cuticular crests are present and the spicules are long and slender. The proposed new Australian genus differs from both of these in the presence and form of the cuticular crests, and in the shape of the bursa. The appearance of the rays is very similar to that figured for *Mammanidula* but in this genus there is apparently one extra ray (or one bifurcated ray) on the left side.

Mastonema is apparently close to *Nippostrongylus* and *Austroheligmonema*. It differs from these in the shape of the spicule, the shape of the bursa and its rays, and in the restricted extent of the cuticular crests.

MASTONEMA MELOMYOS, sp. nov.

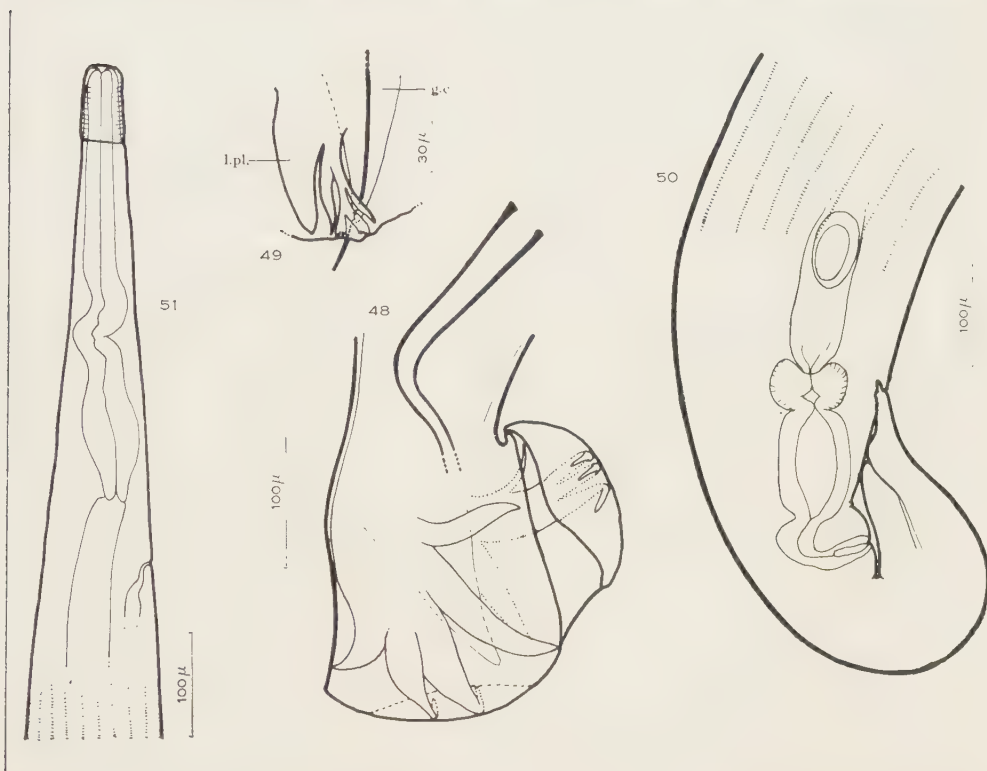
(Figs. 48–51; Table 6)

Host and locality.—*Melomys lutillus*, Whyanbeel.

About 50 large worms obtained from mammary gland. Body curled in 1 (male) or 2 (female) flat coils. Cuticle at anterior end inflated and coarsely annulated. Rest of cuticle striated transversely and longitudinally, the latter especially noticeable towards posterior end of body. Up to 24 longitudinal crests with well-marked transverse striae extend from behind nerve ring to some little distance in front of vulva or bursa. Cervical papillae apparently absent. A number of different-sized irregularly spaced globules underlie cuticle in all specimens. No buccal teeth present.

Oesophagus in all specimens with double kink just posterior to mid-length, widening behind this, narrowing again just before joining intestine. Excretory pore well behind posterior end of oesophagus, relatively further back in male than female. Posterior end of female bent sharply ventrally just behind vulva so that tail points anteriorly. Body narrows quite suddenly in front of vulva and again behind anus; distal half of tail almost cylindrical, with blunt tip. Vulva about two tail lengths in front of anus, eggs, in various stages up to morula, 60–70 μ by 35–40 μ , numerous and small in relation to female body width, compared to those of other trichostrongyles described in this paper.

Bursa asymmetrical, right side larger; dorsal lobe projecting slightly but not otherwise separated from laterals; no dorsal cleft. Bursa traversed by network of fine lines, so much so that details of final branches of dorsal ray obscured. Apart from marked difference in size, main distinction between rays of left and right sides is in posterolateral ray, on right with other laterals and diverging dorsad, on left separate and lying close to and parallel with dorsal ray. Dorsal ray almost



Figs. 48–51.—*Mastonema melomyos*, gen. et sp. nov.: 48, bursa from right side; 49, dorsal, externodorsal, and left posterolateral rays; 50, posterior end of female; 51, oesophageal region; *g.c.*, genital cone; *l.pl.*, left posterolateral ray.

symmetrical, externodorsal of right side a little thinner than that of left. Form of rays shown in Figures 48 and 49. Spicules very thin with narrow alae and simple tips not necessarily joined, though in some specimens lying together. Spicule length about 7–9 times prebursal body width. Gubernaculum about 25 μ long, thin, and not seen in all aspects. Genital cone very long and hard to separate from dorsal wall of bursa. Prebursal papillae not seen.

Family TRICHOSTRONGYLIDAE Leiper

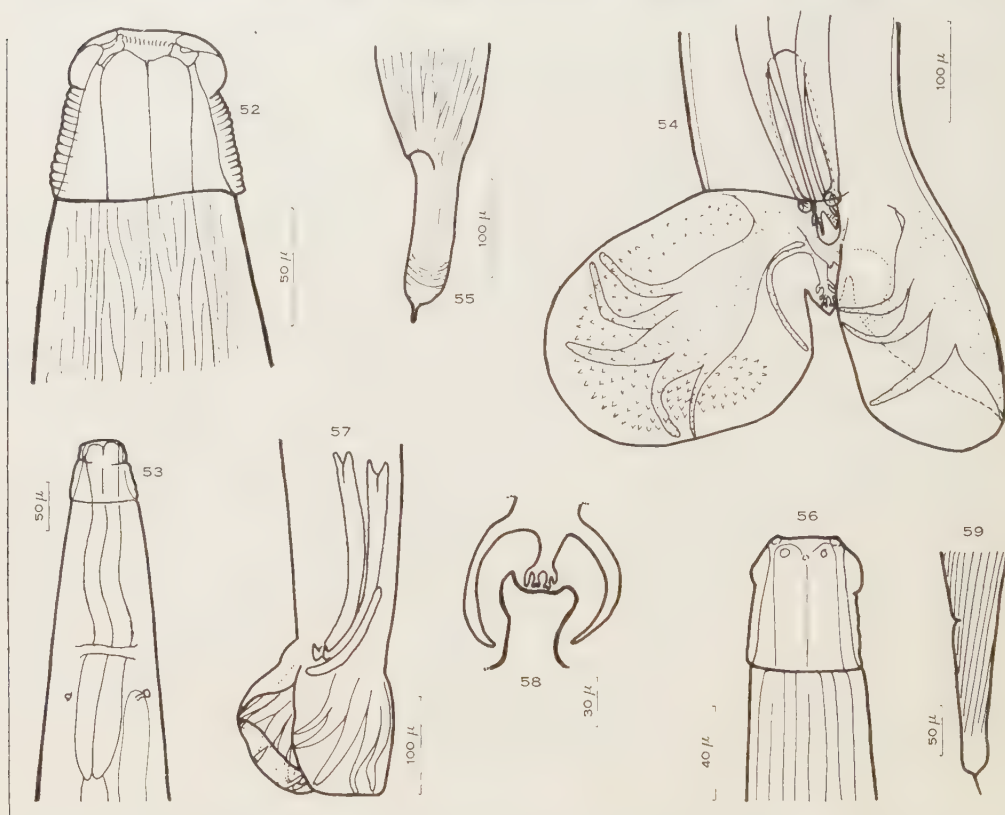
Genus HEPATOJARAKUS Yeh

Hepatojarakus Yeh, 1955, pp. 43–8.

Type species *Hepatojarakus malayae* Yeh, 1955.

Two trichostrongyles have been described from the liver of rats, *Molineus congolensis* Adam & Wanson, 1954, and *Hepatojarakus malayae* Yeh, 1955. These

species are very similar in most respects to each other and to *Molineus* spp. Yeh proposed a new genus for his species because of a "rudimentary corona radiata" around the mouth and because of the greater length of the externodorsal ray. In *M. congolensis* the externolateral ray is short and there is no special structure of the buccal region beyond an annular thickening at the base of the buccal capsule.



Figs. 52-55.—*Hepatojarakus pycnofasciatus*, sp. nov.: 52, head; 53, oesophageal region; 54, bursa, ventral view, one lobe spread out; 55, tail of female. Figs. 56-59.—*H. fasciatus*, sp. nov.: 56, anterior end; 57, posterior end of male; 58, dorsal and externodorsal rays; 59, tail of female.

Two species are described below, from the liver and body cavity of Australian rodents. They also are very close to *Molineus* spp. The externolateral ray is long and the cuticle around the mouth is thickened, and around the shallow buccal capsule is an annular cuticularization, which in some specimens is seen to be faintly striated on the internal surface. The striation might correspond to what is referred to in *H. malayae* as "corona radiata", but is so faint as not to be remarked except in close comparison with Yeh's description. Unfortunately Yeh's figure is too small to show details of this region.

Other differences between *H. malayae* and the two Australian species are the presence of a bifurcation at the proximal end of the spicule and the absence of longitudinal lines on the cuticle, in the former.

HEPATOJARAKUS PYCNOFASCIATUS, sp. nov.

(Figs. 52–55; Table 7)

Hosts and localities.—*Rattus assimilis*, Innisfail (liver, “small intestine”); *Melomys lutillus*, Innisfail (liver).

Large worms, with well-developed cephalic cuticular inflation, divided by annular constriction into 2 parts of which the longer, posterior part is coarsely annulated. Cuticle over rest of body with fine transverse striae, and underlying, very distinct, longitudinal striae, and with numerous fine longitudinal crests on which the transverse striae are more distinct. Only some of these ridges are continuous for most of body length, others arise, bifurcate, and merge in short lengths (Fig. 52). Oesophagus simple, surrounded behind its mid-length by nerve ring; excretory pore and small cervical papillae at same level shortly behind nerve ring.

TABLE 7
MEASUREMENTS OF HEPATOJARAKUS MALAYAE, H. PYCNOFASCIATUS, AND H. FASCIATUS

Part Measured	<i>H. pycnofasciatus</i>	<i>H. fasciatus</i>	<i>H. malayae</i>
Male			
Length (mm)	9.8–11.0	5.9–7.4	6.8–8.6
Breadth (μ)	250	100–140	210–270
Oesophagus (μ)	350–410	320–390	380–420
Anterior end to nerve ring (μ)	200–210	170–200	180–220
Cephalic inflation (μ)	60–65	45–50	—
Spicules (μ)	400–420	190–230	187–230
Gubernaculum (μ)	200	90–100	100–112
Female			
Length (mm)	17.0–19.8	11.1, 12.5	11.9
Breadth (μ)	300–340	230, 200	230
Oesophagus (μ)	440–520	390, 440	—
Anterior end to nerve ring (μ)	210–250	210, 210	—
Cephalic inflation (μ)	60–80	50, 45	—
Posterior end to vulva (% of length)	22–26	28, 26	25
Tail (μ)	160–220	150, —	180

Female tail cylindrical, slightly enlarged rounded tip with short terminal spike. Vulva about one-quarter to one-fifth body length from anus; ovejectors short, opposed. Eggs small and numerous, 60–73 μ by 30–35 μ .

Bursa of two large lateral lobes, beset inside with small rugosities, and short narrow dorsal lobe. Ventral and lateral rays all from same base, all separate and tapering most of their length, the anterolateral distinct from ventrals and other laterals. Externodorsal rays separate, lying in lateral lobes. Dorsal ray bifurcated near tip, each branch dividing again; terminal branches hard to see and in some specimens slightly asymmetrical. Proximal end of each spicule in one view appears to be bifid, in other views 2 apparent rami seen to be connected by curved bars. Distal end of each spicule in two branches, shorter and stouter of which ends in

wing-like expansion, longer blunt. Gubernaculum very strongly built, nearly half as long as spicules, and with distal end hooked ventrally.

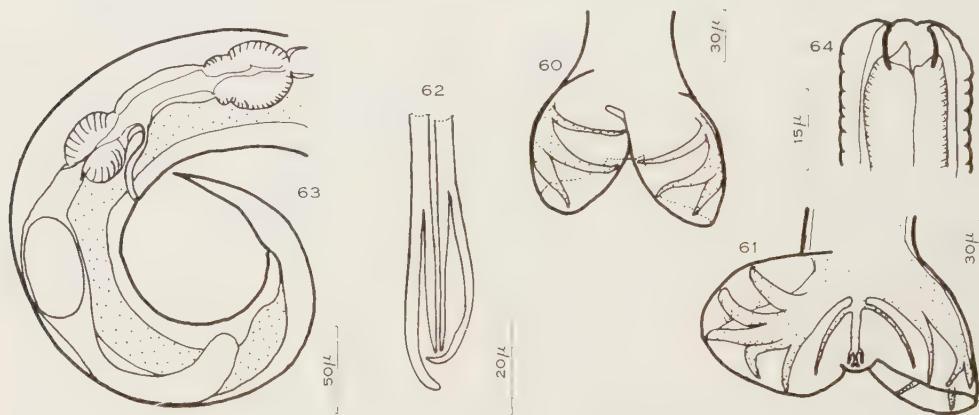
HEPATOJARAKUS FASCIATUS, sp. nov.

(Figs. 56–59; Table 7)

Hosts and localities.—*Rattus conatus*, Innisfail (abdominal mesenteries); *R. assimilis*, Mt. Glorious (peritoneum).

Cephalic cuticle inflated, anterior part wider, unstriated, posterior striated; cuticle of rest of body with 10 (anteriorly) or more (posteriorly) fine cuticular ridges, most of which are continuous throughout body length. Oesophagus more or less cylindrical, surrounded by nerve ring behind its mid-length; excretory pore and cervical papillae short distance behind nerve ring.

Bursa with short slightly indented dorsal lobe, long incurved lateral lobes, lined with large denticles. Rays as shown in Figures 57 and 58. Spicules bifid distally, one branch stouter and longer, ending in ventral hook. Gubernaculum a little less than half spicule length.



Figs. 60–64.—*Austrostrongylus hydromyos*, sp. nov.: 60 and 61, bursa; 62, tips of spicules; 63, posterior end of female; 64, head.

Vulva a little more than one-quarter body length from posterior end. Tail of female digitiform, with tip rounded, slightly swollen, and bearing short spine.

The species is similar to *H. pycnofasciatus*; it is shorter, more slender, and differs mainly in the character of the cuticular ridges, the shape of the tail, the shape of the bursa and form of the bursal rays, and in the shape of the spicules.

AUSTROSTRONGYLUS HYDROMYOS, sp. nov.

(Figs. 60–64; Table 8)

Host and locality.—*Hydromys chrysogaster*, Innisfail.

Very small worms, strongly coiled spirally. Cephalic inflation annulated, rest of cuticle striated transversely; very strongly marked underlying longitudinal

striation, in inflated cuticle as well as elsewhere. Longitudinal ridges restricted to 2 (ventral) over most of body, though in some specimens up to 4 (ventral), in oesophageal region. Distinct somewhat globular buccal capsule present, about 10 μ deep and 8 μ internal diameter; lightly chitinized dorsal tooth present, its tip apparently truncate. Other teeth not seen.

Oesophagus cylindrical; nerve ring not seen; excretory pore and very small cervical papillae at same level, near base of oesophagus.

Bursa symmetrical, dorsal lobe short and small. Arrangement of rays shown in Figures 60 and 61. Spicules stoutly built, somewhat twisted, each ending in 2 branches, one short, slender, and pointed, the other longer, with blunt tip curved inwards, the curved parts of each meeting and giving the whole an appearance of a wide blunt tip. Gubernaculum 50–60 μ long, narrow, elongate, with distal end curved ventrally.

TABLE 8
MEASUREMENTS OF AUSTRONGYLUS HYDROMYOS

Part Measured	Range	No. of Specimens	Mean	Part Measured	Range	No. of Specimens	Mean
Male				Female			
Length (mm)	1.9–2.5	12	2.4	Length (mm)	2.7–4.0	10	3.2
Breadth (μ)	60	2	60	Breadth (μ)	60–70	7	66
Oesophagus (μ)	190–280	11	224	Oesophagus (μ)	220–300	9	259
Anterior end to excretory pore (μ)	180–260	11	197	Anterior end to excretory pore (μ)	180–240	9	203
Cephalic inflation (μ)	55–65	12	57	Cephalic inflation (μ)	55–60	6	58
Spicules (μ)	230–285	12	260	Tail (μ)	55–90	9	76
				Posterior end to vulva (μ)	360–450	10	380

Female with long slender tail narrowing to pointed tip. Vulva about 9–12% of body length in front of posterior end of body. Ovejectors large, posterior one shorter. Eggs 50–65 μ by 25–35 μ .

The species differ from others of the genus mainly in having only ventral longitudinal crests. The cephalic inflation is longer in relation to cephalic diameter than in other species.

PERAMELISTRONGYLUS SKEDASTOS Mawson

Peramelestrongylus skedastos Mawson, 1960, p. 268.

Host and locality.—*Hydromys chrysogaster*, Innisfail (stomach).

This species is a common parasite of bandicoots, in the Innisfail region as well as in other parts of Eastern Australia. This occurrence in a water rat has been noted before (Mawson 1960). The specimens do not differ at all from those described from Innisfail.

ACKNOWLEDGMENTS

I am indebted once more to Dr. M. J. Mackerras, Queensland Institute of Medical Research, for the opportunity to examine parasites of Australian mammals. Dissections of these were made by Dr. Mackerras, Miss M. L. Emanuel, and Miss D. G. Elliot. One collection was sent by Professor J. F. Sprent, Parasitology Department, University of Queensland. Dr. J. L. Harrison, also of the Queensland Institute of Medical Research, kindly sent me information about the biology of the rats around Innisfail.

The names of the rats are those in use by Dr. Mackerras and Dr. Harrison. In naming the new genera and species, I have been greatly helped by Mr. W. A. Cowan, Barr Smith Library, University of Adelaide. Translations from the Russian have kindly been made by Mr. A. Kowanko, Zoology Department, University of Adelaide.

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THE TABANIDAE (DIPTERA) OF AUSTRALIA

IV. SUBFAMILY CHRYSOPINAE

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Summary

The subfamily Chrysopinae is represented in Australia by 1 species of *Chrysops* (Chrysopini) and 36 species of Bouvieromyiini, distributed in the monotypic genera *Phibalomyia* and *Pseudopangonia*, and 4 subgenera of *Mesomyia*, namely: *Lilaea* (6 species), *Perisilvius* (1, a Papuan intrusion), *Pseudotabanus* (*distincta* group 8, *lunulata* group 5, *silvester* group 6), *Mesomyia* (8). Elements of both southern and northern origin are represented.

Most species of *Mesomyia* suck blood; the egg mass of *M. (Pseudotabanus) silvester* (Bergr.) and the larva and pupa of *M. (Lilaea) fuliginosa* (Tayl.) are known.

Distribution of the subfamily in Australia is wide in the Bassian, Torresian, and Eyrean divisions, with a preponderance of species in the north. The semi-arid phases of the Pleistocene climatic cycles are believed to have had a major influence on speciation.

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The following new species of *Mesomyia* are described in the respective subgenera:

Lilaea: *norrisi*, ♀, W.A., ?Vic.

Pseudotabanus: *burnsi*, ♀, N. Qld.; *eyreana*, ♀, W.A.; *fulvissima*, ♀, N.W.A.; *obscura*, ♀, N.T., N. Qld.; *pulla*, ♂ ♀, N.S.W.

Mesomyia: *latifrons*, ♀, ? ♂, S. Aust.; *nigerrima*, ♀, W.A.

Vepriella Mackerras is reduced to the rank of a species group in the subgenus *Pseudotabanus*, and *Mesomyia* (*Pseudotabanus*) *taylori*, nom. nov., is proposed for *distinctus* Taylor nec Ricardo.

I. INTRODUCTION

The Australian Chrysopinae are a compact group of 37 species. Most of them can be identified fairly easily, and there are some clear evolutionary sequences, so that it has been possible to extend the general analysis of speciation to parts of the country not previously covered. The special interest of the subfamily, however, as compared with the Pangoniinae already studied, lies in the evidence it provides for Ethiopian relationship and the existence of an older northern, as well as southern, element in the Australian fauna. I have attempted to re-examine this problem in the light of new knowledge of the Oriental species, but the story is still incomplete. The greatest lack is material from the intervening Moluccan division; but a comparative study of the ecology of the different faunal elements in this country would also be illuminating, and it is hoped that the present paper will provide a foundation for that kind of work.

As in Part III (Mackerras 1960), the species of which the types have been examined personally will be indicated by an asterisk (*) in the citations at the beginning of the descriptions. This will complete the statement of types studied, those of the described Tabaninae having been reviewed in another paper (Mackerras 1959).

My indebtedness to many colleagues has been acknowledged in Parts I and III (Mackerras 1956a, pp. 400-1, 1960, p. 148) in which references to literature before 1960 are also listed.

II. Subfamily CHRYSOPINAE

Ninth tergite divided, a pair of large, characteristically shaped plates in ♂, small, widely separated, triangular plates in ♀. Ocelli well developed. Frons nearly always with shining callus. Basal 4 annuli of 3rd antennal segment more or less completely fused to form a basal plate, followed by a style of 4, occasionally fewer, annuli. Proboscis rarely longer than head height, with large labella. Hind tibiae with paired apical spurs, which are sometimes very short. Basicosta never with strong setulae; vein *sc* setulose or bare; *R*₄ rarely with appendix in Australian species. Style of ♂ hypopygium simple, bluntly pointed in dorsal view. Caudal ends of spermathecal ducts of ♀ simple tubes, without mushroom-like expansions.

Two of the three tribes occur in Australia. The single *Chrysops* is distinctive; but the Bouvieromyiini are remarkably like local Diachlorini (cf. Mackerras 1955b, fig. 3), from which, however, they can always be distinguished by having functional ocelli and hind tibial spurs, as well as by the genitalic characters in both sexes.

As the number of genera and subgenera is comparatively small, it will be convenient to include them all in a single key.

KEY TO GENERA, SUBGENERA, AND SPECIES GROUPS OF AUSTRALIAN CHRYSOPINAE

1. Antennae as long as head and thorax, all segments elongate; small slender species, with broad frons and pictured wings. Tribe CHRYSOPINI *Chrysops* Meig.
Antennae shorter than anteroposterior thickness of head, 1st and 2nd segments less than twice as long as wide; larger or stouter species. Tribe BOUVIEROMYIINI 2
2. Third antennal segment reduced, awl-like, with small plate and 3-annulate style (Fig. 11); very large (18–25 mm), inflated species, with small head and narrow, wrinkled, tomentose frons, without callus (♀ only) *Pseudopangonia* Ric.
Third antennal segment normal, with well-defined plate and 4-annulate style; uninflated species; frons of ♀♀ with clearly defined callus, which is sometimes linear 3
3. Elongate (21 mm), slender, rather wasp-like species; style of hypopygium expanded, semilunate in dorsal view (Fig. 12) (♂ only) *Phibalomyia* Tayl.
Normal, moderately large to small (17–7 mm), diachlorine- or *Tabanus*-like species; style of ♂ hypopygium more slender, tapering *Mesomyia* Macq. 4
4. Eyes hairy, unbanded Subgenus *Mesomyia* Macq.*
Eyes nearly always bare, sometimes banded 5
5. Vein *sc* bare; palp of ♀ expanded basally and with lateral bare area 6
Vein *sc* setulose below; palp of ♀ diachlorine-like, usually without bare area
..... Subgenus *Pseudotabanus* Ric. 7
6. Subcallus shiny; palp of ♀ with long narrow distal prolongation (Fig. 32)
..... Subgenus *Lilaea* Walk.
Subcallus tomentose; palp of ♀ widened at base, acuminate apically (Fig. 50)
..... Subgenus *Perisilvius* End.
7. Eyes of ♀ (in life or relaxed) with 2 bright bands; callus quadrate, with linear extension (Figs. 72–76); 1st antennal segment usually expanded dorsally *lunulata* group
Eyes unbanded; callus of ♀ club-shaped or pyriform (Figs. 56–63, 83–88); 1st antennal segment not expanded dorsally 8
8. Larger (11–16 mm), *Cydistomyia*-like species, with narrow frons (index 3.5 or more), and wings distinctly darkened, at least anteriorly *distincta* group
Smaller (7–11 mm), more slender species, with wider frons (index 2 to 3), and wings usually hyaline *silvester* group

* The hairs on the eyes are short in the ♀ of *M. (M.) doddi* (Ric.); its linear callus will separate it from any of the bare-eyed flies in subsequent captions. Conversely, the eyes are detectably hairy at $\times 15$ in the ♀ of *M. (Ps.) pulla*, sp. nov., but they are banded, the frons is narrower than in the subgenus *Mesomyia*, and the callus (Fig. 76) is differently shaped. The known ♂♂ of the *lunulata* group appear to have only a single band on the eyes.

III. Tribe CHRYSOPINI

Full definition is necessary for Holarctic species only. The characters may be limited here to those of the genus.

IV. Genus CHRYSOPS Meigen

Chrysops Meigen, 1803, *Illiger's Mag. f. Insektenk.* 2: 267. Originally monotypic for *Tabanus caecutiens* Linnaeus, 1758, Palaearctic. No Australian synonymy.

Female

Small slender flies, with patterned wings. Eyes bare; with variegated mottled pattern. Frons wide (index less than 1.5), with transverse callus; subcallus very

short but wide; face smoothly bulging in a characteristic way (Fig. 1), shining. Antennae as long as head and thorax; 1st and 2nd segments more than twice as long as wide. Palpi characteristically tusk-like, partly shining. Proboscis slender; labella relatively small and firm. Fore coxae unusually long, giving the fore legs a somewhat raptorial appearance. Wing with vein *sc* bare; cells R_5 and M_3 widely open; cell Cu_2 narrowly open, or closed on margin. Eighth sternite elongate; caudal ends of spermathecal ducts very slender but strongly chitinated.

Male

Eyes very large, meeting in mid-line; upper facets markedly enlarged, with variegated pattern, sharply separated from the small, dark, lower and posterior facets. Palpi short, subcylindrical. Style of hypopygium moderately slender, smoothly curved.

The Australian species represents the last outpost to the south-east of a relatively recent, world-wide radiation from the Northern Hemisphere, which falls off sharply from about 20 species in the Oriental Region to 3 Austro-Malayan, 2 (1 undescribed) Papuan, and 1 Australian. It does not seem to be particularly close to either of the Papuan species.

CHRYSOPS AUSTRALIS Ricardo

Chrysops australis Ricardo, 1915c, p. 265; Surcouf 1921, p. 150; Taylor 1926, p. 193; Mackerras 1955b, fig. 20, *A, D, J*. Type ♀ ♂, from Herberton, N. Qld., stated to be in the German Entomological Museum. Paratypes in the British Museum (Natural History) agree with specimens in Australian collections.

Psilochrysops australis (Ricardo). Kröber 1929, p. 520, pl. 13, figs. 32, 33, pl. 14, figs. 33, 34.

Material examined.—17 ♂ ♂, 7 ♀ ♀.

A small slender species; with 3rd antennal segment nearly twice as long as 1st and 2nd together; brown scutum; broad brown band and lighter apical darkening on the wings; and brown abdomen, with pale basal band on 2nd tergite, and a median pale stripe from apical half of 2nd to about middle of 5th. Length of head and body 9–11 mm, antennae 3.5–4 mm.

Female (Fig. 1; Plate 1, Fig. 1)

Head.—Frons slightly diverging, index about 1.3, covered in part with grey tomentum and dull cream hairs; a large, raised, bare, but somewhat dull brown callus just above the subcallus, and upper third of frons shining dark brown. Subcallus yellowish grey, tomentose, without hairs; parafacials greyish yellow, variably shiny above tentorial pits, with dull creamy yellow hairs; face shining, light brownish yellow, more definitely brown on lower part, and with rather obscure, pale yellowish hairs in the median area. *Antennae*: 1st segment light yellowish brown; 2nd a little darker, both with short but strong brown hairs; 3rd darker brown. Palpi pale yellowish brown, bare and shining laterally, with light yellowish brown tomentum above and below, and short brown hairs above, creamy yellow ones below. Beard sparse, short, dull cream.

Thorax.—Scutum and scutellum rather a dark brown with a faint violet hue, somewhat unevenly coloured, and with traces of darker median and paler

dorsocentral lines, at least in front of suture; hairs on disc dull cream, inconspicuous, except in front of scutellum where they are yellowish cream; there is a conspicuous brilliant yellow notopleural tuft and another one in the postalar area. Pleura concolorous with scutum, with dull brownish cream hairs, except for 2 further brilliant yellow tufts, one on upper part of the mesopleural convexity and the other above the posterior spiracle.

Legs.—Fore coxae markedly elongate; femora slender; tibiae, especially the anterior ones, distinctly swollen; tarsi normal. All segments light to medium brown, with brown hairs, the tibiae a little darker than the other segments.

Wings.—Ground colour clear; yellowish brown in costal and subcostal cells, and in narrow streaks basally along *R* and *Rs* anteriorly and *Cu*₁ posteriorly; a broad dark brown band extending completely across wing from apices of basal cells to about level of tip of *R*₁; beyond this the apex of the wing is a lighter greyish brown, separated from the darker colour by a narrow clear area. Stigma indefinite; veins yellowish to yellowish brown in the clear parts, dark brown in the darker part.

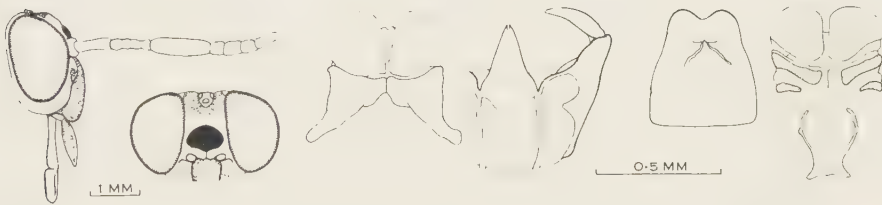


Fig. 1.—*Chrysops australis* Ric.: head of ♀, ♂ genitalia, ♀ genitalia.

Abdomen.—Moderately deep brown; base of 1st tergite clear yellowish cream; base of 2nd translucent cream, narrowly in the median line and broadening laterally to the posterior margin of the tergite, so that the brown colour is reduced to a half-moon shape on disc and a narrowly darkened lateral margin; a creamy yellow median vitta extending from about middle of 2nd tergite into apical half of 5th; hairs short, brown on the darker areas, cream to creamy yellow on the paler areas; marginal zone not strongly developed. Venter with 1st, 2nd, and part of 3rd sternite light translucent yellowish cream, with inconspicuous cream hairs; remainder rather a dark brown, a little paler along apical edges, and with dark brown hairs.

Male (Fig. 1)

Resembles ♀ in coloration and markings, but distinctly paler. Eyes large, upper enlarged facets variegated yellow and dark brown or black, lower ones uniformly dark. Palpi short, subcylindrical, with fairly long brown hairs, and not showing the shining lateral areas seen in the ♀.

Distribution.—QUEENSLAND: Kuranda, Dodd; Cairns, Mar.; Meringa, Nov., Goldfinch, Taylor.

This species, unlike many *Chrysops* in other parts of the world, appears to be uncommon, and nothing is recorded of its habits or life history.

V. Tribe BOUVIEROMYIINI

Large to small, mostly diachlorine-like or *Tabanus*-like species. Eyes bare or hairy; sometimes banded, but never mottled in life. Subcallus longer and narrower than in Chrysopini; face more truncate, rarely shining. Antennae shorter than anteroposterior diameter of head; 1st and 2nd segments little, if at all, longer than wide. Palpi not tusk-like nor shining. Proboscis usually stout, with large labella. Fore legs not raptorial. Wing with vein *sc* setulose or bare; cells *R*₁ and *M*₃ open (in Australian species); cell *Cu*₂ closed, petiolate. Genitalia unspecialized in ♀, occasionally modified in ♂.

Dias and Sousa (1957) have proposed the name Erodiorhynchini to replace Bouvieromyiini, on the principal ground that it is founded on the oldest included generic name. While I agree entirely with Oldroyd's (1957) dissatisfaction with Bouvieromyiini — based on a new name for a homonym which is now a subjective synonym in an outlying, specialized part of the tribe! — there was no available alternative under the "Copenhagen Decisions", 1953, paragraphs 45 (1), 49 (2), and 54 (1), except Scarphiini Enderlein, 1922, which was equally unsatisfactory. The action of Dias and Sousa was not admissible under the "Decisions", so it would seem that Bouvieromyiini must remain the name of the tribe, at least until the new "*Règles*" are published.

Origins and Relationships

The distribution of the Bouvieromyiini in the faunal regions of the world is illuminating:

	No. of Species		No. of Species
Palearctic	1	Ethiopian	64
Nearctic	3	Oriental	9
Neotropical	2	Australasian	41

We are, thus, dealing with a third essentially southern tribe, but differing from the Pangoniini and Scionini already reviewed, in that the strongest link is between Australia and Africa, rather than between Australia and South America.

The evidence is partly numerical, only two species of the tribe being known in South America,* but there is morphological evidence as well. I was able recently to make a brief survey of the Ethiopian material in the British Museum, and was impressed by the many points of resemblance between both bare-eyed and hairy-eyed species in Africa and Australia. There were differences, to be discussed below, and locally developed endemic elements in both faunas; but the strongest general impression was of close phyletic relationship and common evolutionary capacities.

There is another significant difference between the tribes, in that the Pangoniini and Scionini are essentially southern in Australia, with no more than

* *Mesomyia* (*Coracella*) *carbo* (Macq.) — formerly known as *Mesomyia* (*Veprius*) *presbiter* Rond. — and *M. (C.) rubricornis* (Kröb.) (see Philip 1960, p. 71). The types of the other two Neotropical species that might have been Bouvieromyiini, *Silvius rufipes* Macq. and *Silvius rufopilosus* Big., proved on examination to be Pangoniini.

minor northern extensions, whereas there appear to be separate southern and northern elements in the *Bouvieromyiini*.

The southern element is the smaller, and comprises the subgenus *Mesomyia* with 8 Australian and 5 South African species, the genus *Pseudopangonia* as an offshoot from it in Australia, and endemic offshoots also in Africa. Their distribution suggests an Antarctic link, and there is nothing to add to what has already been written about it (Mackerras 1955*b*, 1956*a*; Oldroyd 1957). The northern element requires more detailed examination.

When Part I of this series (Mackerras 1956*a*) was prepared, I had seen too few Ethiopian species to have much confidence in "marker" characters which might indicate the origin of a particular element, and there was a wide gap around the Indian Ocean between elements that were undoubtedly of African origin and others that might have been of Australian origin. This led to the suggestion that the then known extensions might represent a "pincer movement" from the two regions. That idea I now believe to be wrong.

In the first place, there are two characters which do tend to distinguish Ethiopian from Australian *Bouvieromyiini*. The more consistent is the absence of setulae on vein *sc* of the wing. All *Pangoniinae* have *sc* bare, and all *Tabaninae* have it setulose, at least below; it is only in *Chrysopinae* that the character has differential value. Within that subfamily, all *Chrysopini* examined have *sc* bare, and all *Rhinomyzini* have it setulose. In the *Bouvieromyiini*, all Ethiopian and Oriental species have *sc* bare, and so have the Palaearctic *Thaumastomyia* and the Nearctic *Merycomyia*, which appear to have been derived from originally Ethiopian stock (Philip and Mackerras 1961). The only known exception is the presence of a few setulae distally on the lower surface of *sc* in 2 of 3 *Paulianomyia rufa* Oldr. from Madagascar. In the Australasian region, the vein is bare in three primitive species of the subgenus *Mesomyia*, the monotypic genus *Phibalomyia*, the subgenus *Lilaea*, the Papuan subgenus *Pareucompsa*, and two other Papuan species (*vittata* Ric. and *demeijerei* Ric.) which I had previously included in *Pseudotabanus*. On the other hand, a strong series of setulae is present, at least on the lower surface of *sc*, in the five remaining Australian species of the subgenus *Mesomyia*, the one known species of *Pseudopangonia*, all species of the subgenus *Pseudotabanus*, and in the Neotropical *M. (Coracella) carbo* (Macq.).

The other indicator is a tendency for the palpi of the females to be expanded basally, with a clearly defined, often depressed, lateral bare area. This form of palp is not universal in Ethiopian species, but it occurs commonly, for example, in the subgenera *Mesomyia*, *Perisilvius*, and *Rhigioglossa*, and in both subgenera of *Aegophagomyia*. It is also seen in the Oriental *Eucompsa*, the Papuan *Pareucompsa*, *M. vittata* and *M. demeijerei*, and the Australian *Lilaea*, but rarely (1 species of subgenus *Mesomyia*, 2 of the *silvester* group) in other Australian members of the tribe, and not in the South American subgenus.

It is unlikely that two, presumably independent characters would appear so consistently together in the Oriental-Australasian groups, as a combined result of survival of a primitive venational character and parallel evolution of a

specialized palpal character. It seems more probable that they do indicate relationship, and that *Eucompsa*, *Pareucompsa*, *vittata* and *demeijerei*, and *Lilaea* belong to the eastern end of a northern arc of migration from Africa. For this reason, I have now allotted *vittata* and *demeijerei* to the subgenus *Perisilvius*, where, indeed, they seem to be better placed than in *Pseudotabanus* or *Lilaea*. *Phibalomyia* cannot be considered further until the female is discovered.

The second reason why the earlier suggestion must be abandoned is that the wide gap in distribution from Madagascar (Rodriquez I., for *Aegophagomyia*) to Borneo, no longer exists. It has been filled, in quite a remarkable way, by the genus *Gressittia*, which is close to *Mesomyia*, neatly homogeneous, and has the



Fig. 2.—Distribution of Bouvieromyiini around the Indian Ocean: ● *Mesomyia* (*Perisilvius*); ▲ *Gressittia*; ○ *Eucompsa*; ◐ *Mesomyia* (*Pareucompsa*).

following distribution (Philip and Mackerras 1961): Kenya (1 species), India (1 species, with an offshoot of 1 species in Nepal and 1 in central China), Malaya (3 species), Sumatra (1 species). The arc is completed by *Eucompsa*, with 1 species in Borneo and 1 in Java, *Pareucompsa*, with 2 species in New Guinea, *Perisilvius*, with 20 Ethiopian and 2 Papuan species, one of which extends down the coast of Queensland, and *Lilaea*, with 6 species in Australia. The distribution, except for *Lilaea* (Fig. 4), is shown in Figure 2, which may be compared with Figure 3 in Mackerras (1956a).

This arc carries no particular implications in relation to past migration across what is now the Indian Ocean, because it exists around the ocean at the present day, and migration could have followed the indicated pathway during the long periods of relatively uniform world climate in the first half of the Tertiary, as well as during shorter periods subsequently. The earlier waves must be assumed to have been quite ancient, to account for the degrees of differentiation that have occurred in *Eucompsa*, *Pareucompsa*, and *Lilaea*. It would be tempting to regard Miss Cheesman's (1951) "Cyclopea" as having provided the Tertiary bridge from the Oriental region, but the distribution in Figure 2 does not fit that hypothesis.

very well, and it must be left for further consideration until the Tabaninae have been examined.

The subgenus *Pseudotabanus* has still to be considered. It is more difficult, and its three species groups are best treated here as separate entities. They all have an essentially northern distribution, but they lack those "markers" which distinguish the northern elements already discussed.

The *distincta* group is probably the oldest, and it could have arisen in three different ways:

- (i) Its close resemblance to the South American *Coracella*, which is doubtfully separable from it subgenerically, suggests that it might already have been separated from ancestral *Mesomyia* (s.l.) before Australia became isolated in the Mesozoic. Its essentially northern distribution (Fig. 5), however, is against that hypothesis.
- (ii) It could have been separated from ancestral *Mesomyia* (s.s.), perhaps by the Cretaceous seas, after isolation of the continent, the characters it shares with *Coracella* being the result of parallel evolution. There is no morphological impediment to this hypothesis, which may receive some support from the rather wide distribution of its more primitive members.
- (iii) In spite of its differentiating characters, it could have been derived from Ethiopian stock, and followed the same path as *Lilaea*, but in an earlier wave which has left no trace.

The second seems, on present knowledge, to be the most reasonable of these hypotheses and the third the most speculative. Whichever may be correct, it seems highly probable that ancestral *Cydistomyia*-like forms with setulae on *sc* were established in Australia well before the end of the Tertiary.

The *lunulata* and *distincta* groups have so much in common that they must be presumed to have been derived from a common ancestor. It would fit the distributional and morphological evidence, if the ancestral population had been split at the Gulf of Carpentaria by the mid-Pliocene aridity (see Mackerras 1960) in the same way that later populations appear to have been divided by the interglacial aridities (Fig. 10).

The *silvester* group, on the other hand, seems more likely to have been derived independently from southern *Mesomyia*. The relatively wide, usually diverging frons and shape of callus in the female and the genital style of the only male known (cf. Figs. 24 and 29 or 30) suggest this, and the present status of the group in *Pseudotabanus* is based rather on convenience than on phylogeny. It also could have been segregated by the mid-Pliocene aridity, but from the south by a latitudinal barrier, rather than meridionally in the north.

The story is still tantalizingly incomplete, but the present indications are that our bouvieromyiine fauna was built up in the following ways at about the times suggested:

Of southern origin

Mesomyia (*Mesomyia*) — interregional (Mesozoic)*Pseudopangonia* — local (?Cretaceous or Tertiary)

Possibly southern

Mesomyia (*Pseudotabanus*) — local*distincta* group (?Cretaceous)*lunulata* group (mid-Pliocene aridity)*silvester* group (mid-Pliocene aridity)

Possibly northern

Phibalomyia — local (Tertiary)

Of northern origin

Mesomyia (*Lilaea*) — local (Tertiary)*Mesomyia* (*Perisilvius*) — interregional (Pleistocene or Recent)*Habits and Seasonal Occurrence*

Nothing is recorded about the behaviour of *Phibalomyia carteri*, of which only males have been collected, nor of *Pseudopangonia australis*, which is known from only 5 ♀♀ collected more than 50 years ago.

Most females of *Mesomyia* have been taken when attempting to suck blood, but a few have been found resting on bushes, although they do not seem to be particularly attracted to flowers. Some, especially species of the *lunulata* group in the Northern Territory, are attracted to warm motor-car tyres, flying around them, alighting, and attempting to probe the rubber, as if it were the skin of a host. The attraction declines when the tyres cool down.

These species behave just like the common Tabaninae, and some of them are quite vigorous in their attacks. Ferguson and Henry (1920) recorded *M. (Lilaea) lurida* as occurring commonly on cattle and horses, especially round the hooves, at Kendall, N.S.W., and *M. (L.) paralurida* as biting the fetlocks of cows and horses in the same locality. Both species also attack man, at least when larger hosts are not near. Mr. J. H. Calaby (personal communication) noted that the species he encountered in Western Australia (mainly *M. (L.) fuliginosa* and *M. (L.) norrisi*) showed a predilection for boot-leather, and wondered whether shoes were to be regarded as analogous to hooves. No attraction to rabbits or other small hosts has been observed.

Further north, *M. (Ps.) silvester* and *M. (M.) montana* commonly attack man in southern Queensland, as does *M. (Ps.) queenslandi* north of Innisfail, but I have not known them to reach the pest abundance of some of the smaller species in the Northern Territory. Of these, at least *M. (Ps.) tryphera* (specimens collected by A. R. Woodhill) can induce sensitization, indurated lumps developing at the sites of the bites and persisting for several days. Some subjects are said to become febrile. I was first told of this phenomenon by the late J. A. Gilruth, and others have reported it since, so it seems to be fairly common, but it is not clear whether it is specific to *tryphera*, or whether other species can produce it as well.

The seasonal occurrence of the adults is shown in Figure 3. There is a clearly defined summer distribution, with little difference between the subgenera, in south-eastern Australia, but both the northern and south-western distributions appear to be more diffuse. In the north, which includes all records north of the Tropic, this is due to the *lunulata* group occurring mainly in spring and the *distincta* and *silvester* groups mainly in summer, with *M. (L.) fuliginosa* on the wing in autumn and spring (Apr.–Nov.), and the gap partly filled by the related

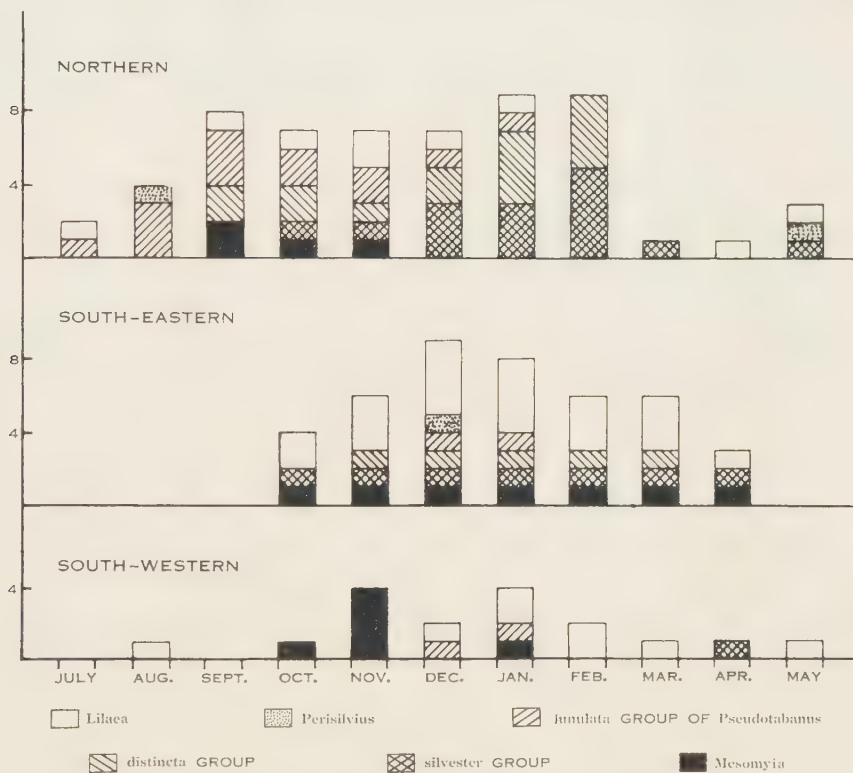


Fig. 3.—Seasonal occurrence of subgenera and species groups of *Mesomyia*.

M. (L.) mansoni (Nov.–Jan.). In the south-west, the scatter is largely due to *M. (L.) fuliginosa* and *M. (L.) norrisi*. Indeed, *M. (L.) fuliginosa* has been taken, in different parts of its range, in every month except June.

The only other evident trend is that the species of the subgenus *Mesomyia* tend to show the displacement towards the spring in the north and west that is characteristic of the old southern element in the fauna.

Life History

Taylor (1917a) has described the egg mass of *M. (Ps.) silvester*. He found it, as the fly finished ovipositing, on a blade of grass at the edge of running water in a small, sandy creek at Townsville, and described it as follows:

"Very long and narrow, measuring 29 mm., by an average of 1.5 mm. and contains a very large number of eggs, which are a light amber-brown, cylindrical, and pointed like a cigar at the apex, and measure 1.3×0.2 mm. (vix)."

The specimen is in the School of Public Health and Tropical Medicine, University of Sydney.

Johnston and Bancroft (1920*b*) found full-grown larvae of *M. (L.) fuliginosa* in muddy sand at the edge of the Burnett R. in south Queensland, and Hill (1921) collected prepupae of the same species in nearly dry, stiff loamy soil, at 10–30 cm below the surface, about 12 ft from the water's edge in the bank of a pool at Townsville. Larvae collected by both authors pupated readily in pots of sand, flies emerging from 8 to 14 days (Hill) to about a month later (Johnston and Bancroft).

The full-grown larva is about 33 mm long, creamy white, with "orange-citrine" bands on most segments, and a transverse ridge and pseudopods on the first 7 abdominal segments (Hill 1921). The 8th abdominal segment is conical, and has a protrusible spiracular spine, like that of *Chrysops*. Other features which distinguish it from other known tabanid larvae in Australia are: all segments longitudinally striate; prothoracic annulus evenly rugose all over; antennae with apical segment longer than penultimate, which is short, squat, and less than twice as long as wide; mandibles strong, blunt-ended; 8th abdominal segment without fleshy or chitinous processes round the spiracular area.

The pupa is 18–20 mm long, and quite like the pupae of unspecialized Tabaninae, with all 3 pairs of processes on the aster moderately developed. It can be distinguished by having the spines on 3rd to 5th abdominal tergites more or less in a single row, mostly short with broad bases and dark tips, but some with long bristles, and the 8th segment without dorsolateral combs.

As in previous Parts, I am indebted to Miss K. M. I. English for the morphological details given here.

Distribution

The general patterns of distribution are evident from the maps, so we may limit this account to an analysis of the species of *Mesomyia* and their inter-relationships, as a foundation for the discussion of speciation in the next section.

Subgenus *Lilaea*

The pattern (Fig. 4) is dominated by the extraordinarily wide distribution of *fuliginosa*, which is rivalled among Australian members of the family only by *Tabanus townsvilli* Ric. (Mackerras, 1961, fig. 5). Underlying this, there is a division into two series: the grey species, *mansoni* and *fuliginosa*, in the north; and the brown species, *lurida* and *paralurida* (also *stradbrokei*, if it is distinct from *paralurida*), on the east coast, with the western *norrissi* morphologically intermediate between *lurida* and *paralurida*. The occurrence of *norrissi* in western Victoria is anomalous, but I am not completely happy about the identification of the single female seen.

All the species appear to be limited to high-rainfall country, except *fuliginosa*, which extends deeply into the Eyrean division from southern Queensland to western Victoria. As pointed out in the earlier (1961) paper, however, this may not be as extreme as it appears, because the flies are found mainly within the flood-banks of the rivers, where the humidity is relatively high, and there is water in which they can breed. Except for their absence from Tasmania and high country on the mainland, there is no indication of primary adaptation to Torresian or Bassian climate.



Fig. 4.—Distribution of the subgenus *Lilaea*: ▲ *fuliginosa* (Tayl.); △ *masoni* (Sum.); × *stradbrokei* (Tayl.); ● *lurida* (Walk.); ○ *paralurida* (Ferg. & Henry); ○ *norrisi*, sp. nov. Arrows on east coast mark approximate positions of the Burdekin, Fitzroy, Brisbane, and Cassels gaps.

Subgenus *Perisilvius*

The Australian distribution of *demeijerei* is shown in Figure 2. It is fairly abundant in New Guinea, but rather rare in Australia.

Subgenus *Pseudotabanus*

The *distincta* group (Fig. 5) is dominantly tropical, and almost completely limited to humid country. There is one outlying species in Western Australia, two pairs in the north, and an allopatric series down the east coast.

The species may be divided into three series on abdominal pattern. What appears to be the basic pattern consists of dark brown tergites, with rather broad pale apical bands more or less completely divided by a diffuse black median vitta or chain of blotches. *M. (Ps.) grandis*, *taylori*, *fuscipennis*, and *distincta* have abdomens of this type (Plate 1, Fig. 6), and the series can be further subdivided on wing pattern and shape of callus. In the second series, melanism has obscured the pattern, resulting in almost completely black abdomens, with relatively narrow pale apical bands on the tergites. *M. (Ps.) ater*, *nigripennis*, and possibly *fergusoni*



Fig. 5.—Distribution of the *distincta* group, subgenus *Pseudotabanus*: × (N.W.A.) *grandis* (Ric.); △ (N.T.) *ater* (Tayl.); ▲ (N.Qld.) *nigripennis* (Ric.); ▼ (N.T.) *taylori*, nom. nov.; ▽ (N.Qld.) *fuscipennis* (Ric.); ● (N.Qld.) *queenslandi* Ric.; ○ (C.Qld.) *distincta* Ric.; △ (S.Qld. N.S.W.) *fergusoni* (Ric.).

belong here; but *fergusoni* has a narrow frons and callus and relatively well-defined scutal vittae, which suggests that it may have evolved independently from *distincta* stock. The third series contains only *queenslandi*, which is distinguished by the median black blotches being split by intrusive, pale apical triangles (Mackerras 1956a, plate 1, fig. 9); otherwise it is closely related to *distincta*. The suggested evolution of the species is shown diagrammatically in Figure 6.

The *lunulata* group (Fig. 7) includes two divergent species, *pulla*, which is apparently restricted to a small patch of high country in New South Wales, and *equina*, which is widely but thinly scattered in the north, and three (possibly more)

closely related northern species. *M. (Ps.) lunulata* and *frontalis* are sympatric in the Northern Territory, but *lunulata* extends further to the west, and *frontalis* pairs with *burnsi* on the east coast.

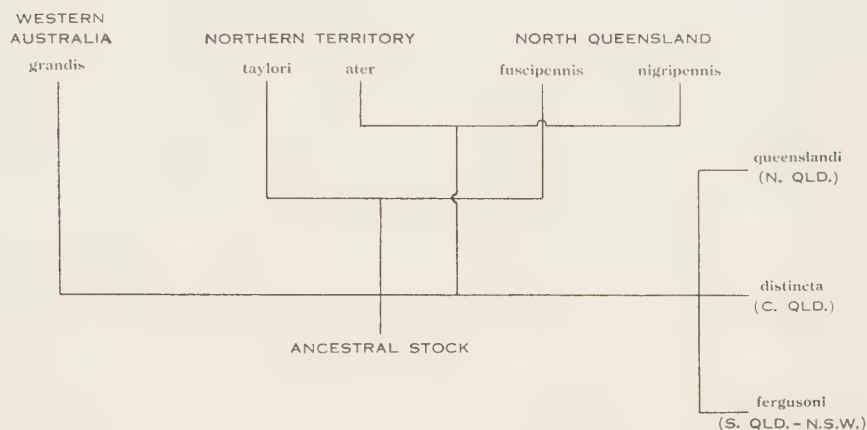


Fig. 6.—Diagram of the suggested evolution of the *distincta* group, subgenus *Pseudotabanus*, arranged to show the distribution of the species.



Fig. 7.—Distribution of the *lunulata* group, subgenus *Pseudotabanus*: ● *lunulata* (Big.); ○ *frontalis* (Ric.); ▽ *burnsi*, sp. nov.; ▲ *equina* (Ferg. & Hill); △ *pulla*, sp. nov.

The *silvester* group (Fig. 8) is slightly more complicated. Its most divergent member is *fulvissima* in north-western Australia, followed by the *alcocki* (N.T.)–*obscura* (N.T., N. Qld.) pair, which is clearly distinguished from the remaining *tryphera* (N.T.)–*silvester* stock. *M. (Ps.) silvester* seems to be almost as adaptable as *M. (L.) fuliginosa*—indeed, there are two quite typical specimens from the centre of the continent—and the western *eyreana* appears to have been derived from it.



Fig. 8.—Distribution of the *silvester* group, subgenus *Pseudotabanus*: ▼ *fulvissima*, sp. nov.; ▲ *alcocki* (Sum.); △ *obscura*, sp. nov.; ○ *tryphera* (Tayl.); ● *silvester* (Bergr.); ○ *eyreana*, sp. nov.

Subgenus Mesomyia

This subgenus is undoubtedly ancient, and the pattern of distribution (Fig. 9), apart from its predominantly Bassian form, is complicated by the existence of three presumably relict species, *latifrons* and *tepperi* in South Australia and *cydister* in Western Australia. *M. (M.) imitator* and *nigerrima* form a related, sympatric pair in the west, the north-eastern *doddi* is very close to the south-eastern *montana*, and the more distinct, western *sulcifrons* was clearly derived from *montana* stock.

The Problem of Speciation

The thesis that environmental changes in the Pleistocene provided the conditions for a great deal of speciation in the Tabanidae has been developed in two earlier papers (Mackerras 1960, 1961), and the Bouvieromyiini received some consideration in the second one. Consequently, the present discussion may be confined to a summary and extension of what was written then.

The evolutionary background has been discussed on pp. 832-6, to which it is only necessary to add that three archaic species of the subgenus *Mesomyia* (*cydister*, *latifrons*, *tepperi*), as well as the ancestors of the *imitator-nigerrima* pair and of the *montana* complex, had probably achieved reproductive isolation long before the period with which we are now concerned. Like the Pangoniini,



Fig. 9.—Distribution of the subgenus *Mesomyia*: ○ *doddi* (Ric.); ● *montana* (Ric.); ▽ *tepperi* (Ferg.); ▼ *latifrons*, sp. nov.; ○ *sulcifrons* (Ferg.); × *cydister* (Tayl.); ▲ *imitator* (Ferg.); △ *nigerrima*, sp. nov.

they cannot be fitted into any pattern that is at present recognizable. It is possible, too, that division of *Lilaea* into “grey” and “brown” segregates may date from the mid-Pliocene aridity, but it could equally have occurred during the first interglacial, and all the remaining speciation in the tribe seems to have taken place from that time onwards. It can be summarized conveniently in four divisions.

Southern

In contrast to *Scaptia*, there is no evidence that the Tasmanian land bridges or the glacial periglacial wedges have had any effect on speciation in Bouvieromyiini, and there appears to have been comparatively little traffic between south-eastern and south-western Australia. Only in *Lilaea* is the typical pattern seen in *lurida* (eastern) → *norrissi* (western) → *paralurida* (eastern). In the subgenus *Mesomyia*, the ancestors of *sulcifrons* probably spread to the west in the first or second Australian glaciation, for it is well differentiated, and a sequence *nigerrima* (W.) → ?(E. or S.A.) → *imitator* (W.) may be presumed to account for these two sympatric relatives.

Northern

Most of the speciation in the tribe has occurred in this segment, which has been described in the 1961 paper. The glacial pattern was of continuous fertile country, perhaps broken in places by rain-forest, and the interglacial pattern is illustrated in Figure 10.

In *Lilaea*, *fuliginosa* and *masoni* are closely related to each other, and they probably became separated at the Gulf of Carpentaria in the last interglacial. There was subsequent diffusion both ways, and widespread extension of *fuliginosa* through south-eastern Australia to Flinders I. and across to the south-west (Fig. 4), the last stage possibly occurring during the recent "little ice age". There is considerable variation within this species, but no clear indication of subspeciation.



Fig. 10.—The probably habitable areas in northern Australia during Pleistocene interglacials (stippled), as indicated by the present 40-in. isohyet. Broken line, present 25-in. isohyet. From Mackerras (1961) by permission of the Council of the Royal Society of Victoria.

The *distincta* group of *Pseudotabanus* (Figs. 5 and 6) provides the most striking evidence of any so far studied. The ancestral population was probably widely diffused across the north, and was divided into *grandis* (western), *taylori-fuscipennis* (central), and residual stock (eastern) by the first interglacial. Following diffusion in the next glaciation, the second interglacial divided *taylori* (N.T.) from *fuscipennis* (N. Qld.) and *ater-nigripennis* (N.T.) from residual *distincta* stock (N. Qld.). Again there was diffusion, and the third interglacial separated *ater* (N.T.) from *nigripennis* (N. Qld.). This sequence, which implies that there may be a missing relative of *distincta* still to be discovered in the Northern Territory, now seems more probable than segregating the *ater-nigripennis* stock in Cape York as suggested in the 1961 paper.

The *lunulata* group (Fig. 7) is more complex. The ancestors of *pulla* and *equina* may have been segregated early in (or even before) the Pleistocene, and the residue contains a complex of variable, sympatric forms which are difficult to sort out. However, it seems likely that *lunulata* and *frontalis* stocks were segregated

in the western and central divisions, respectively, during the second interglacial, with subsequent almost complete mixing of populations, but separation of *burnsi* (N. Qld.) from *frontalis* (N.T.) by the third interglacial. The remarkable extension of *lunulata*, apparently unchanged, to south-western Australia may have occurred during the last glaciation (or conceivably in the "little ice age"), when the arid belt was at its narrowest.

The *silvester* group (Fig. 8) shows a pattern more like that of the *distincta* group, except that the moisture requirements of the species appear to be less strict, and there has consequently been more diffusion and mixing of populations. It is suggested that a widely dispersed ancestral population was divided by the first interglacial into the ancestors of *fulvissima* (N.W.A.), *alcocki-obscura* (N.T.), and *tryphera-silvester* (N. Qld.), and the second separated *alcocki* (N.T.) from *obscura* (N. Qld.) and *tryphera* (N.T.) from *silvester* (N. Qld.). The *silvester* stock probably spread widely across Australia in the last two glacial phases, and retreated in the interglacial and postglacial phases, leaving pockets occupied in favourable country, an earlier one giving rise to *eyreana*, and later ones providing the scattered pattern of present Eyrean distribution that is illustrated.

Papuan

Exchange of species has been slight. An ancestral form related to *M. (Ps.) queenslandi* reached New Guinea, probably in the penultimate glaciation, and differentiated there into a recognizably distinct, undescribed species; and the Papuan *M. (P.) demeijerei* migrated to Australia unchanged, presumably during the last glaciation. *Chrysops australis* was presumably derived also from Papuan ancestors during the Pleistocene.

Eastern

Only two small series remain to be considered. One is the residue of the *distincta* group, three neatly allopatric species, which are still separated by the Burdekin and Fitzroy gaps, as they no doubt were when the gaps were better defined in the penultimate or last interglacial (Mackerras 1961). The other includes the long series of variable montane and coastal forms in the subgenus *Mesomyia*, extending from southern New South Wales to north of Cairns. They may well become divided into a series of discrete entities in the next arid phase, but at present I can distinguish only the northern *doddi* from the remaining *montana* stock, the break having probably been at the Burdekin gap in the last interglacial, with later northern diffusion of *montana*.

Conclusion

The combination of Scionini (Mackerras 1960) and Bouvieromyiini almost completes the picture of Pleistocene speciation, as it has been possible to visualize it in this one family. There are unexplained species in both groups, but most of them appear to be old, probably relict forms which do not really belong to the sequences that have been discussed. On the whole, the correlation between the morphological, distributional, and palaeoclimatological evidence has been good, and it now remains to test the conclusions further by an independent analysis of the Tabaninae.

VI. Genus PSEUDOPANGONIA Ricardo

Pseudopangonia Ricardo, 1915c, p. 273; Surcouf 1921, p. 135; Enderlein 1925, p. 318; Ferguson 1926a, p. 300; Oldroyd 1947a, p. 138; Mackerras 1955b, p. 612. Monotypic for *Pseudopangonia australis* Ricardo, 1915, Queensland.

Female

A large, inflated, soft-bodied, dull-coloured insect, with unusually small head and very short soft proboscis. Eyes bare; unbanded. Frons narrow, parallel, longitudinally wrinkled, tomentose, without callus. Subcallus moderately bulging, tomentose, without hairs; face hollow, with very large and deep tentorial pits, tomentose, and unusual in being almost without hairs. Antennae (Fig. 11) greatly modified; 1st segment inflated, a little longer than wide; 2nd cup-shaped; 3rd little more than half as wide as 2nd, awl-like, its basal plate evenly swollen, and the style slender, truncate apically, and consisting of 2 annuli and an indication of a 3rd. Palpi as long as shaft of proboscis, tapering, rather soft and hairy. Legs rather long, moderately stout; hind tibial spurs short but strong. Wings large; vein *sc* setulose below. Hypopygium rather broad and flattened; caudal ends of spermathecal ducts wide, lightly chitinized.

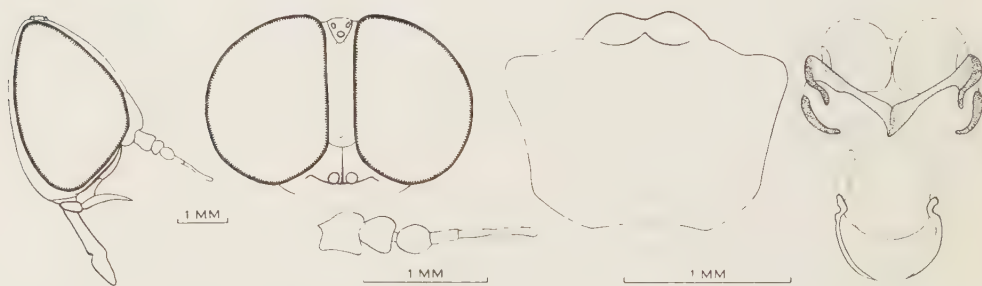


Fig. 11.—*Pseudopangonia australis* Ric., ♀. Enlarged antenna drawn from a cleared specimen.

This is probably the most aberrant genus in the tribe. It shows some superficial resemblance to *Thaumastomyia* Leclercq recently described from China; but the morphology of the head and genitalia suggest that it originated locally from ancestral *Mesomyia* stock, and probably from that part of it that gave rise to the *montana* complex. It seems possible that its unusual features may have developed during a long period of equable conditions in the Tertiary, and that it is now a relict.

PSEUDOPANGONIA AUSTRALIS Ricardo

* *Pseudopangonia australis* Ricardo, 1915c, p. 274; Surcouf 1921, p. 136; Mackerras 1955b, p. 612, fig. 17. Type ♀, from Burpengary, S. Qld., T. L. Bancroft, in the British Museum (Natural History). The type is larger (25 mm), in better condition, and more richly coloured than the other specimens I have seen, but there is little doubt that it is conspecific with them.

Material examined.—5 ♀♀.

A large, hump-backed, soft-bodied, light yellowish brown species; with small head; uniformly light brown wings; and brown legs. Length 18–25 mm.

Female (Fig. 11; Plate 1, Fig. 2)

Head.—Frons narrow (index 5), with light brownish fawn tomentum, irregularly brownish and with a few short hairs in middle. Subcallus rather protuberant, with light brownish tomentum, without hairs; parafacials and face light creamy fawn, with only a few short cream hairs near lower margin. *Antennae*: 1st segment light creamy fawn, 2nd brown, both with brown hairs; 3rd not much longer than 1st and 2nd together, brown. Palpi short, brown, with brown hairs, except for some cream ones below on 1st segment. Proboscis with unusually conspicuous cream hairs on shaft and brown ones on labella. Beard sparse, creamy white.

Thorax.—Scutum and scutellum yellowish brown to fawn-brown, with dull, light brown hairs. Pleura similar, but with cream to dull yellowish cream hairs.

Legs.—Coxae light fawn-brown, with dull creamy white hairs; remaining segments moderately dark brown, with mainly dark brown to blackish hairs.

Wings.—Long, parchment-like, uniformly light brown; veins light brownish yellow.

Abdomen.—Soft; ground colour similar to scutum, and with dull brown hairs; sublateral areas on 1st 4th tergites brighter yellow, with golden hairs, and lateral areas rich brown, with brown hairs. Venter pale creamy fawn with a greyish hue, apices and lateral margins of sternites cream; hairs short, creamy white. In the type, the abdomen is brighter yellow basally, with brown median vitta and lateral margins, and becoming more diffusely brown on 4th and subsequent tergites.

Distribution.—QUEENSLAND: Burpengary, Bancroft. NEW SOUTH WALES: Richmond R., Jackson; Clarence R., Froggatt. (No dates given.)

VII. Genus PHIBALOMYIA Taylor

Elaphromyia Taylor, 1917a, p. 749, 1917b, p. 517. Monotypic for *Elaphromyia carteri* Taylor, 1917, Queensland. Not *Elaphromyia* Bigot, 1859 (Diptera, Trypanidae).

Phibalomyia Taylor, 1920, p. 165, nom. nov.; Ferguson 1926a, p. 300; Mackerras 1955b, p. 611.

Male

A long slender insect, with rather wasp-like coloration and markings. Eyes bare; unbanded; touching in mid-line, with some frontal hairs showing between them; upper facets not enlarged. Subcallus moderately bulging, tomentose, with hairs on each side; face (Fig. 12) triangularly produced at middle, of unusual shape, shiny. Antennae with normal large basal plate and 4-annulate style. Palpi very short; 2nd segment about equal to 1st, subcylindrical, with a dorsal bare area, and fairly strong hairs. Proboscis rather slender, a little longer than head-height, with well-developed firm labella. Legs long, rather slender; hind tibial spurs long. Wing with vein *sc* bare; cell *R*₅ somewhat narrowed. Style of hypopygium markedly expanded to an almost half-moon shape (Fig. 12).

Only three males are known.

PHIBALOMYIA CARTERI (Taylor)

* *Elaphromyia carteri* Taylor, 1917a, p. 749. Type ♂, from Kuranda, N. Qld., F. P. Dodd, in the School of Public Health and Tropical Medicine, University of Sydney. The other 2 ♂♂ are in the British Museum (Natural History).

Phibalomyia carteri (Taylor). Mackerras 1955b, p. 611, fig. 16.

Material examined.—3 ♂♂.

A large, narrow-bodied, wasp-like species; with bright orange legs; largely flavid wings; and yellow abdomen, marked with black. Length 21 mm.

Male (Fig. 12; Plate 1, Fig. 3)

Head.—Eyes small but wide, touching about middle of frons, slightly diverging above and below. Frontal triangle and subcallus continuous, bright yellow, with yellowish cream tomentum, and short creamy yellow hairs lateral to antennae; parafacials velvety, deep golden, with bright golden hairs; face dull golden, thinly tomentose on upper half, more shining below, and with some brown hairs on either side of mid-line. *Antennae*: basal segments light yellowish brown, with a slight

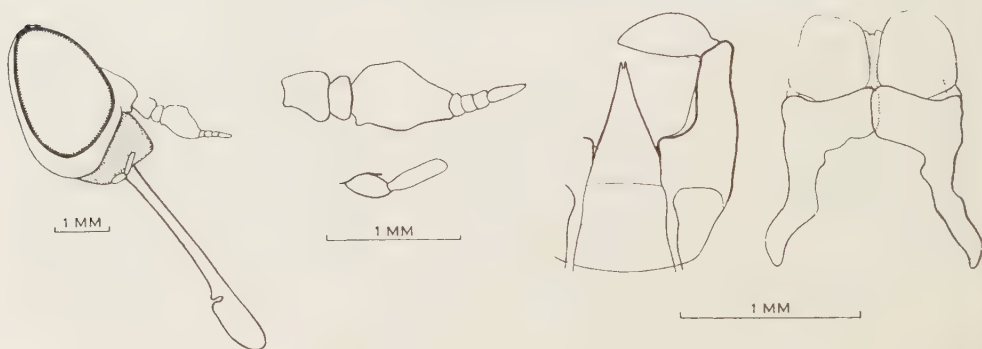


Fig. 12.—*Phibalomyia carteri* (Tayl.), ♂.

cream overlay and short brown hairs; 3rd bright orange, with some brown hairs sub-basally on basal plate and occasional very short ones on style. *Palpi*: 1st segment light greyish brown, with brown hairs; 2nd very short, rounded apically, and with quite strong, deep brown hairs. Proboscis brown to somewhat reddish brown, with short but quite conspicuous brown hairs laterally and below, and a zone of golden hairs basally above. Beard moderately developed, bright golden.

Thorax.—Scutum rather variegated; dark olive in the median area, bright yellowish fawn laterally and on the shoulders, and with a blending of pale fawn and olive in the dorsocentral lines; there is also a narrow, dark brown, post-sutural median line, which widens markedly in front of the scutellum, and deep olive brown to blackish brown markings occupying about half the sublateral area in front of suture and almost the whole of it behind. Hairs fairly long, dull creamy gold, denser and brighter laterally. Scutellum deep reddish brown, somewhat brighter laterally and at apex, and with dull golden hairs. Pleura with pronotal lobes bright yellow, with dense long golden hairs; remainder dark greyish olive, becoming dark brown on upper part of upper mesopleural convexity, and with

dull creamy gold hairs, except for a patch of brighter golden ones above the posterior spiracle.

Legs.—Bright orange, except for the mid and hind coxae, which are greyish; hairs bright golden, darkening somewhat on the apical segments.

Wings.—Somewhat greyish, strongly suffused with yellow anteriorly and along the veins, giving the wing a somewhat variegated, flavid appearance. Stigma inconspicuous; veins bright orange-brown, somewhat darker distally.

Abdomen.—Creamy to bright yellow; with a large median dark brown mark on 1st tergite, a triangular one extending from base to apex of 2nd, and remaining tergites with broad, dark to blackish brown basal bands which are expanded to form median and lateral triangles. Hairs golden on the paler parts, brown on the darker; marginal hairs moderately developed, creamy gold. First sternite and extreme base of 2nd pale translucent greyish cream; remainder deep brown, with pale greyish cream lunules laterally on 2nd to 4th.

Distribution.—QUEENSLAND: Kuranda, Dodd; Herberton, Nov., Dodd.

VIII. Genus MESOMYIA Macquart

Mesomyia Macquart, 1850, p. 37; Mackerras 1955*b*, p. 591; Oldroyd 1957, p. 202.

Originally monotypic for *Mesomyia decora* Macquart, 1850, Ethiopian. No Australian synonyms, except the erroneously applied "*Silvius*" of earlier authors.

This genus includes all the more generalized species, which lack the distinctive modifications that have been used to separate other genera in the tribe. There is, nevertheless, considerable variation among them, so they have been broken up (Mackerras 1955*b*; Oldroyd 1957) into 1 subgenus in South America, 6 in Africa, and 5 in Australia and New Guinea. It will, therefore, be convenient to give detailed definitions under the subgenera, rather than to attempt a comprehensive definition here. The female genitalia are more useful at the specific than at the subgeneric or group level; but those of the males (Figs. 13–30) show some suggestive minor differences and resemblances, so they have been grouped in a single block for comparison.

Four of the Australasian subgenera occur in Australia; the fifth (*Pareucompsa* End.) is limited to New Guinea. Three (*Pareucompsa*, *Lilaea*, *Mesomyia*) are clearly defined by characters that are easy to see; they should present little difficulty to a worker in the field. The other two (*Perisilvius* and *Pseudotabanus*) are distinguished from one another by less evident characters, but I believe that they represent separate lines of evolution, which it is necessary to recognize, if our understanding of the tribe is to be extended.

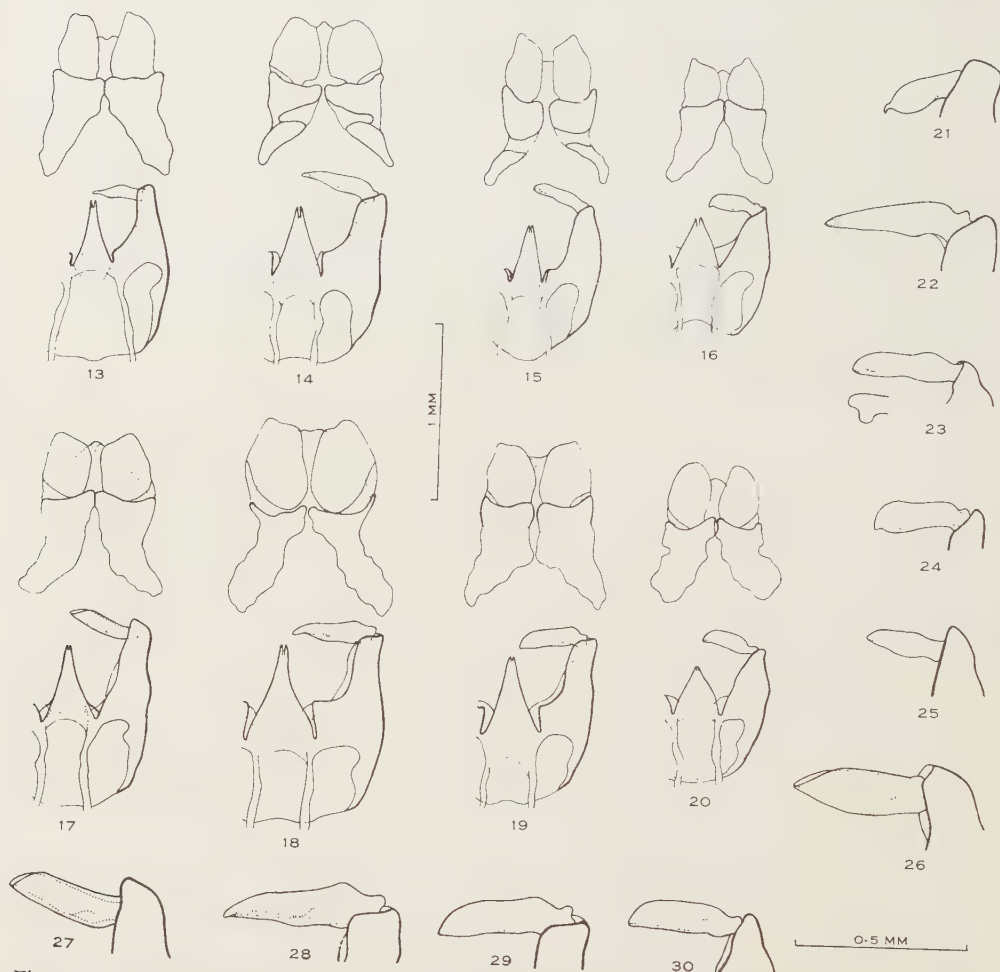
Subgenus LILAEA Walker

Lilaea Walker, 1850, p. 11; Surcouf 1921, p. 125; Ferguson 1924, p. 254, 1926*a*, p. 294; Oldroyd 1947*a*, p. 140; Mackerras 1955*b*, p. 606. Type species *Pangonia lurida* Walker, 1848, Australia, by selection of Coquillett 1910, p. 561. Not Enderlein 1922, p. 341, 1925, p. 297 (= *Scaptia* (*Pseudoscione*), see Mackerras 1960, p. 81).

Ommia Enderlein, 1922, p. 348, 1925, p. 339. Monotypic for *Ommia prisca* Enderlein, 1925, Victoria. The type ♀ of *O. prisca*, received through the kindness of Professor F. Peus, proved to be identical with *M. (L.) lurida* (Walker).

Female

Mostly medium-sized to large, smooth, *Tabanus*-like flies, with clear wings. Eyes bare; usually unbanded. Frons medium (index 2.5–3.5), converging, occasionally almost parallel; callus relatively small, narrower than frons, and often



Figs. 13–20.—Male genitalia of *Mesomyia*: 13, *M. (Lilaea) mansoni* (Sum.); 14, *M. (Pseudotabanus) nigripennis* (Ric.); 15, *M. (Ps.) lunulata* (Big.); 16, *M. (Ps.) silvester* (Bergr.); 17, *M. (Mesomyia) sulcifrons* (Ferg.); 18, presumed ♂ of *M. (M.) latifrons*, sp. nov.; 19, *M. (M.) cydister* (Tayl.); 20, *M. (M.) imitator* (Ferg.). Figs. 21–30.—Styles of *Mesomyia*: 21, *M. (L.) fuliginosa* (Tayl.); 22, *M. (Ps.) nigripennis*; 23, *M. (Ps.) lunulata*, with diagrammatic view of ventral lobe; 24, *M. (Ps.) silvester*; 25, *M. (M.) doddi* (Ric.); 26, *M. (M.) montana* (Ric.); 27, *M. (M.) sulcifrons*; 28, *M. (M.) latifrons*; 29, *M. (M.) cydister*; 30, *M. (M.) imitator*.

restricted to its lower half, sometimes inconspicuous. Subcallus prominent, shining, sometimes highly polished, without hairs. Face tomentose. First antennal segment not enlarged; 3rd with broad basal plate and 4-annulate style. Palpi (Fig. 32) characteristic, very long, attenuate, and with a well-defined concave lateral bare

area. Proboscis strong. Wings with vein *sc* bare. Caudal ends of spermathecal ducts wider and more prominent than in other subgenera.

Male

Eyes very large, *Tabanus*-like; with a narrow blue-green band at the junction between the conspicuously enlarged upper and small lower and posterior facets. Palpi short and plump, rounded apically. Genitalia with style of hypopygium tapering to a point and without ventral lobe (Figs. 13 and 21).

The essential features of this exclusively Australian subgenus are the bare eyes, shining subcallus, absence of setulae on *sc*, and the characteristic palpi of the females. The species fall into two series, which are distinguished in the first caption of the key. They are easily recognizable on fresh material, but older specimens tend to become greasy in a way that cannot be removed with amyl acetate, and these may cause difficulty, because it is often necessary to rely on their head characters only.

KEY TO SPECIES OF THE SUBGENUS LILAEA

Females

1. Subcallus blackish brown, highly polished; greyish or yellowish species2
 Subcallus brighter brown, more or less shining, but not highly polished; brown species3
2. A larger (11–14 mm), broader, greyish species; scutal vittae clearly defined; abdomen with a pattern of median and lateral whitish apical triangles on tergites. Widely distributed*fuliginosa* (Tayl.)
 A smaller (9–12 mm), more slender, yellowish species; scutal vittae evanescent; abdomen more or less completely yellowish basally, darkened apically. Northern Territory, north Queensland*mansoni* (Sum.)
3. A large (14–17 mm), broadly built, robust species; frons relatively wide (index about 3); callus irregular, and not usually reaching mid-length of frons; median and lateral pale apical triangles on abdominal tergites conspicuous. South Queensland to Victoria*lurida* (Walk.)
 Less broadly built, usually somewhat smaller species; frons narrower (index about 3.5); callus extending beyond middle of frons4
4. A darker species; callus and antennal plate dark brown to black; abdominal pattern as in *lurida*. Western Australia, ?Victoria*norrisi*, sp. nov.
 Brighter brown species; callus and antennal plate bright brown; median triangles on abdomen small, and lateral triangles reduced to apical fringes on tergites. Eastern coastal5
5. A more robust, darker brown species, with wider callus (Fig. 40), and dark greyish brown scutum*paralurida* (Ferg. & Henry)
 A more slender, lighter brown species, with narrow callus (Fig. 41), and bright reddish brown scutum*stradbrokei* (Tayl.)

MESOMYIA (LILAEA) FULIGINOSA (Taylor)

- * *Silvius notatus* Ricardo, 1915c, p. 264; Taylor 1919, p. 43; Johnston and Bancroft 1920, p. 129, figs. 7, 8 (pupa); Ferguson 1920, p. 132, 1921a, p. 368; Ferguson and Hill 1920, p. 461, 1922, p. 245; Hill 1921, p. 59, figs. 19–21 (larva and pupa); Surcouf 1921, p. 143; Enderlein 1925, p. 314. Type ♀, from Kalamunda, W.A., March, in the British Museum (Natural History). Not *Silvius notatus* (Bigot, 1892), Nearctic, as noted by Ferguson and Hill (1922) and Philip (1941).

* *Silvius fuliginosus* Taylor, 1916, p. 810; Ferguson and Hill 1920, p. 461 (probable syn. of *notatus* Ricardo). Type ♀, from Stapleton, N.T., 1.v.1913, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney. The identity with *notatus* is confirmed from a comparison of further specimens from the Northern Territory.

Mesomyia (Lilaea) fuliginosa (Taylor). Mackerras 1956a, p. 378.

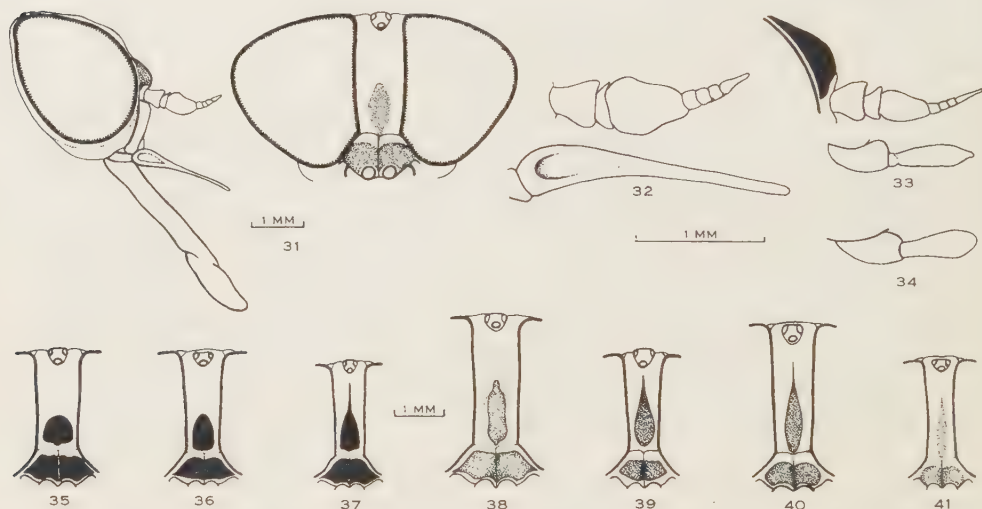
* *Silvius psarophanes* Taylor, 1917b, p. 520; Ferguson and Hill 1920, p. 461 (syn. of *notatus* Ricardo). Type ♂, from Townsville, N. Qld., F. H. Taylor, in the School of Public Health and Tropical Medicine, University of Sydney.

Silvius abrus Philip, 1941, p. 187, nom. nov. for *notatus* Ricardo nec Bigot.

Mesomyia (Lilaea) abra (Philip). Mackerras 1955b, p. 606, fig. 13.

Material examined.—25 ♂♂, 79 ♀♀.

A variable, dark brownish grey species; with grey vittae on scutum; grey to yellowish brown femora and tibiae; and pale median and lateral triangles on abdominal tergites. Length 11–14.5 mm.



Figs. 31–41.—Subgenus *Lilaea*, ♀♀, except 33 and 34: 31, 32, 38, *lurida* (Walk.); 33, *mansoni* (Sum.), subcallus, antenna, and palp of ♂; 34, *fuliginosa* (Tayl.), palp of ♂; 35 and 36, *fuliginosa*, showing variation in shape of frons; 37, *mansoni*; 39, *norrisi*, sp. nov.; 40, *paralurida* (Ferg. & Henry); 41, *stradbrokei* (Tayl.).

Female (Figs. 35–36, 42–44)

Head.—Frons relatively wide, index about 2.5, with fawn-brown tomentum and short dark brown hairs; a pale grey area around the grey ocellar triangle, and a narrow light creamy fawn zone between the blackish brown callus and the highly polished, deep mahogany to blackish brown subcallus. Lower part of subcallus pale grey tomentose around and at sides of antennae; parafacials and face pale grey, both with quite long, dense, greyish white hairs and some brown ones. **Antennae:** 1st and 2nd segments fawn-grey to brown, with black hairs; 3rd dark brown. **Palpi:** 1st segment fawn-grey, with silvery and a few brown hairs; 2nd brown, with short but strong black hairs around the bare area. Beard greyish white.

Thorax.—Scutum dark brownish grey, with narrow pale grey median line, broader pale grey dorsocentral vittae, which may become confluent in front of scutellum, and lateral areas grey, with a patch of brown above wing root; hairs appressed dull cream to yellowish, and fine erect black; notopleural hairs mixed black and greyish white; supra- and postalar tufts greyish white. Scutellum grey, darker in median zone, with dull golden appressed hairs, some silvery ones laterally, and mixed black and greyish white marginal hairs. Pleura pale grey, with greyish white hairs, mixed with some brown to black ones on upper mesopleural convexity.

Legs.—Femora variable, grey to light fawn-brown with more or less greyish overlay, with greyish white and some dark hairs; tibiae fawn-brown, variably darkened on apical half or more, especially of fore pair, and with greyish cream hairs on the paler parts, dark brown elsewhere; hind tibial fringes short but fairly dense, mixed black and greyish cream; tarsi deep brown to blackish, with black hairs.

Wings.—Greyish; stigma brown; veins light to deep brown.

Abdomen.—Dark brownish grey, somewhat variegated, with short dark brown hairs; base and lateral area of 1st tergite paler grey, and apices and lateral margins of remaining tergites light creamy to yellowish grey; apical hairs greyish white on the lateral third of the tergites, brown in the intermediate zone, and greyish white to yellowish cream on the small but sharply defined median triangles. Venter grey, variably suffused with brown, with apices of sternites cream, and with short white hairs, variably mixed with black in median zone.

Male (Figs. 21, 34; Plate 1, Fig. 4)

Similar to ♀, but more hairy, and ground colour of abdomen more variegated. Eyes very large, meeting over most of frontal length; large upper facets sharply differentiated from the small, dark, lower and posterior facets, and separated from them by a narrow green band. Palpi yellowish fawn to brown, with dark brown hairs and some greyish white ones below.

Older specimens, including the types of *fuliginosa* (♀) and *psarophanes* (♂), are paler than those described above, and so are some more recent ones from north-eastern Queensland. Some of the darker specimens have gonopophyses of the form shown in Figure 43, but there was no correlation between coloration and form of gonopophyses, nor with width of frons, which varied appreciably in both northern and southern specimens. Only dark forms with gonopophyses as in Figure 44 are known so far from Western Australia, but much longer series would be necessary to determine whether there are any real racial differences within the species.

Distribution.—NORTHERN TERRITORY: Margaret R., Marrakai, July, Mackerras and Campbell; Stapleton, May, Hill; Roper R., Apr. O'Gower. QUEENSLAND: Mitchell R. Mission, Apr., biting, M.J.M.; Townsville, Oct., Nov., Hill, Taylor; 35 miles SW. of Ayr, Oct., Riek; 15 miles W. of Bowen, Sept., Riek; Springsure, Feb., Mercer; Eidsvold, Dec., Feb., Apr., Bancroft. NEW SOUTH WALES: Moree, Nov., Mar., Dyce; Brewarrina; Bourke, Oct., Paramonov; Narrabri, Feb., White; Nyngan (Bogan R.), Armstrong; Collie, Apr., Key and Chinnick; Trangie, Nov., Dec., Froggatt, Perry; Warrah, Froggatt; Penrith, Dec.; Sydney (Herne Bay), Feb., Gibbons, McMillan; Wentworth, Dec., M.J.M.; Yenda, Jan.; Hay, Jan., Froggatt; Deniliquin, Feb. VICTORIA: Mildura, Jan., Dobrotworsky; Robinvale, Mar., Nikitin;

Lake Hattah, Nov., J.E.D.; Sea Lake, Mar., Goudie; Kerang, Mar., R.T.; Echuca, Jan., Wilson; Jeparit, Feb., Common; Lah Arum and Mt. Difficult Ra., Grampians, Feb., Common; Wilson's Promontory, biting man, Feb., Douglas. FLINDERS I.: Scott's Lagoon, Jan., Calaby. WESTERN AUSTRALIA: Mt. Helena, Aug., L. Wilson; York, Dec., Calaby; Kalamunda, Mar.; Dryandra, Feb., Calaby; Burekup, Jan., Calaby; Bowelling, Jan., Calaby.

MESOMYIA (LILAEA) MANSONI (Summers)

- * *Silvius mansonii* Summers, 1912, p. 226; Ricardo 1915c, p. 259 (misspelt *marsoni*); Taylor 1916, p. 806; Surcouf 1921, p. 143; Enderlein 1925, p. 314. Three cotype ♀♀, from Darwin, N.T., Strangman, formerly in the London School of Hygiene and Tropical Medicine, now in the British Museum (Natural History). These three specimens appear to be conspecific.

Mesomyia (Lilaea) mansonii (Summers). Mackerras 1955b, p. 606.

- * *Silvius strangmani* Summers, 1912, p. 227; Ricardo 1915c, p. 259 (misspelt *strangmanni*); Taylor 1916, pp. 806, 815; Surcouf 1921, p. 143; Enderlein 1925, p. 314. One cotype ♀, from Darwin, N.T., in the British Museum (Natural History), another (not seen) understood to be in the London School of Hygiene and Tropical Medicine. The former, which is conspecific with the cotypes of *mansonii* Summers, is now chosen as lectotype.

- * *Silvius sordidus* Taylor, 1916, p. 808; Ferguson and Hill 1920, p. 462, 1922, p. 251. Type ♀, from Batchelor, N.T., 2.xii.1912, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney. Specimens agreeing with it were conspecific with the cotypes of *mansonii* Summers.

- * *Silvius tabaniformis* Taylor, 1916, p. 813; Ferguson and Hill 1920, p. 462 (syn. of *sordidus* Taylor). Type ♀, from 30 miles E. of Darwin, N.T., 11.xii.1914, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

- * *Silvius subluridus* Taylor, 1917a, p. 752; Surcouf 1921, p. 143; Ferguson and Hill 1922, p. 251 (syn. of *sordidus* Taylor). Type ♀, from Darwin, N.T., on horse, 13.i.1914, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—1 ♂, 12 ♀♀.

Distinguished from *fuliginosa* by smaller size, more slender build, paler antennae, avittate scutum, light fawn legs, and largely yellowish brown abdomen. Length 9–12 mm.

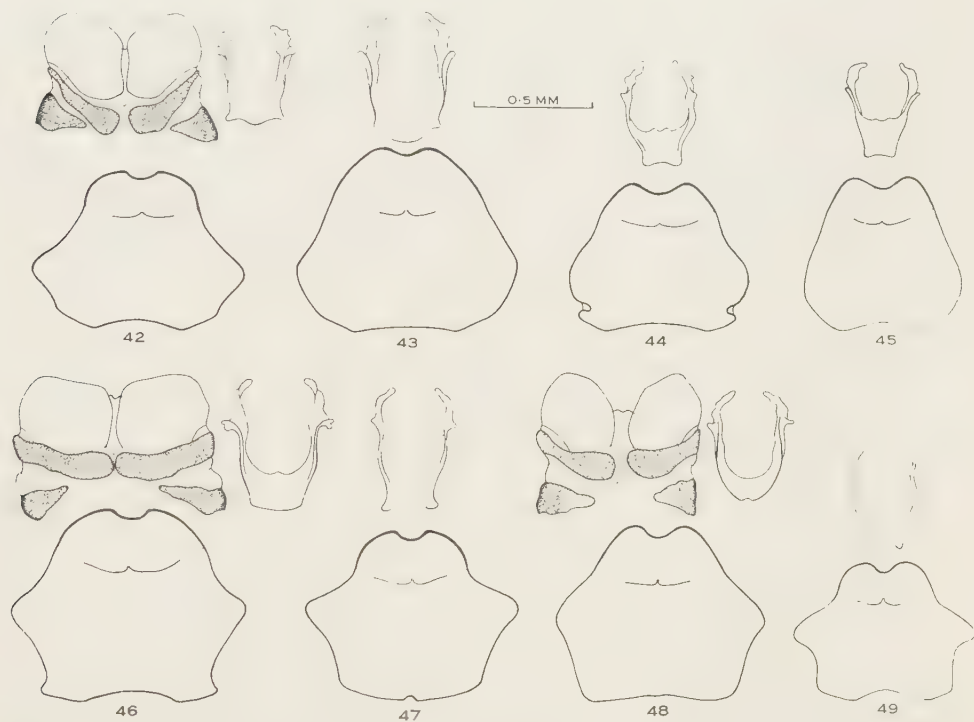
Female (Figs. 37, 45)

Head.—Frons narrower than in *fuliginosa*, index 3, with fawn tomentum, sometimes with a greyish hue, and short dark hairs; callus highly polished, mahogany to blackish brown, pear-shaped, tapering to a point at its upper end. Subcallus polished, mahogany to blackish brown, except for narrow margin along eye and at sides of antennae; parafacials and face light grey, with a patch of short brown hairs on upper part of parafacials, greyish white ones elsewhere. *Antennae*: 1st and 2nd segments creamy yellow, with cream hairs below, some strong black ones above, and a narrow rim of short black hairs around apex of 2nd segment; 3rd bright yellowish brown. Palpi light yellowish brown, darker at extreme tip, and with mainly cream hairs. Beard greyish to creamy white.

Thorax.—Scutum and scutellum grey, almost without vittae, but somewhat darkened in median area and in sublateral areas behind suture; lateral areas in front of suture and shoulders light creamy fawn; hairs short appressed dull gold,

and a few inconspicuous erect darker ones; marginal hairs mixed black and greyish white in front of suture, cream elsewhere. Pleura light grey, with greyish white hairs, mixed with a few black ones on upper part of upper mesopleural convexity.

Legs.—Coxae grey, with greyish white hairs; femora pale yellowish brown, with variable greyish overlay and cream hairs; tibiae light yellowish brown, with creamy golden hairs; tarsi darker brown, with brown hairs.



Figs. 42-49.—Subgenus *Lilaea*, ♀ genitalia: 42-44, *fuliginosa* (Tayl.), type ♀, one from Marrakai, N.T., and one from York, W.A.; 45, *masoni* (Sum.); 46, *lurida* (Walk.); 47, *norrissi*, sp. nov.; 48, *paralurida* (Ferg. & Henry); 49, *stradbrokei* (Tayl.).

Wings.—Slightly greyish; stigma brown, inconspicuous; veins light brown to yellowish.

Abdomen.—Yellowish brown, paler on apices of tergites, and irregularly darkened in patches, especially on 4th and subsequent tergites; hairs cream to pale creamy gold, mixed with black on the darker areas. Venter yellowish, variably suffused with grey, especially apically; all sternites paler on their apical edges; hairs cream, except for black on last segment. The degree of darkening on the abdomen varies, but altogether this species is more yellowish than *fuliginosa*.

A ♀ from Groote Eyelandt has a narrow oblique blue-green band on the eyes, which showed up both on relaxation and in Goffe's solution; but it does not differ otherwise from the remaining ♀♀, in which no signs of a band could be detected.

Male (Figs. 13, 33)

A single ♂ in the Berlin Museum, labelled "Nord Australien", is about the same size (12 mm) as the type of *subluridus*, and agrees with it very well.

Eyes wider than thorax, swollen, meeting on full length of frons; upper facets markedly enlarged, brown, with hairs just perceptible at $\times 15$, sharply marked off from the small, black, lower and posterior facets, which extend to the vertex in a narrowing posterior band. The specimen was not relaxed to determine the presence of a band on the eyes. Ocellar tubercle prominent, brown; frontal triangle yellowish fawn, tomentose; subcallus swollen, shining dark brown, except for creamy fawn tomentose zone around and lateral to insertions of antennae. Parafacials and face pale grey, with greyish white hairs, and a few dark ones laterally on parafacials. Palpi with 1st segment swollen, 2nd somewhat spindle-shaped, both brownish yellow, with white hairs (dark in ♂ *fuliginosa*). Hind tibial spurs very short.

Distribution.—NORTHERN TERRITORY: Darwin, Dec. Jan., on horse, Hill, Strangman; 30 miles E. of Darwin, Dec., Hill; Batchelor, Dec. Hill; Stapleton, Dec., Hill; Groote Eyelandt, Tindale. QUEENSLAND: Cardington Stn., Nov., Norris.

MESOMYIA (LILAEA) LURIDA (Walker)

* *Pangonia lurida* Walker, 1848, p. 140; Ricardo 1900a, p. 121 (considered to be a tabanine); Surcouf 1921, p. 128 (as ?*Pangonius*). Type ♀, from Port Stephens, N.S.W., in the British Museum (Natural History).

Lilaea lurida (Walker). Walker 1850, p. 11; Oldroyd 1947a, p. 140.

Silvius luridus (Walker). Ricardo 1915c, p. 260 (as *lurida*); Taylor 1917a, p. 752; Ferguson 1920, p. 132; Ferguson and Henry 1920, p. 838; Ferguson and Hill 1922, p. 250.

Mesomyia (Lilaea) lurida (Walker). Mackerras 1955b, p. 606, fig. 13.

* *Silvius hackeri* Taylor, 1919, p. 45; Ferguson and Hill 1922, p. 250 (syn. of *lurida* Walker). Type ♀, from Brisbane, 15.xi.1916, H. Hacker, in the Queensland Museum, Brisbane.

* *Ommia prisca* Enderlein, 1925, p. 339. Type ♀, from Melbourne, in the Berlin Museum. Not a synonym of *Ectenopsis (Parasilvius) victoriensis* Ferguson, as thought by Ferguson 1926a, p. 305, and Mackerras 1956b, p. 431 (see Mackerras 1960, p. 146).

Material examined.—48 ♀♀.

A large, robust, dark brown species; with fairly evident scutal vittae; and white-haired median spots and lateral patches on abdominal tergites. Length 14–17 mm.

Female (Figs. 31, 32, 38, 46)

Head.—Frons medium, index 3, with fawn to brownish tomentum, and short black hairs; callus brown, rather inconspicuous, of irregular shape and extent, most definite on about one-third the width of the frons in its lower third, and tapering variably above that point. Subcallus shining, variegated brown, margined with light creamy fawn tomentum; parafacials and face light creamy to fawn grey, with creamy white hairs mixed with some brown ones. *Antennae*: 1st and 2nd segments pale creamy brown, with black hairs; 3rd dark brown, paler at extreme base. Palpi light yellowish brown, with mixed black hairs and some cream ones at base. Beard creamy white.

Thorax.—Scutum brown, darkened in median and sublateral areas, so that the more greyish dorsocentral vittae and lighter brown lateral areas show up fairly clearly; hairs long, dull cream and dark brown, stronger on margins. Scutellum reddish brown, darker basally, and with dark brown and dull cream hairs, the latter especially strong around margins. Pleura pale fawn with greyish reflections; hairs long and dense, cream, mixed with some dark brown, especially on upper part of upper mesopleural convexity.

Legs.—Coxae greyish fawn, with creamy white hairs; remaining segments bright brown, darkening on tarsi.

Wings.—Slightly greyish; stigma inconspicuous; veins bright brown.

Abdomen.—Rich brown, sometimes rather variegated, paler on apical edges of tergites; hairs dark brown on most of abdomen, with, in perfect specimens, small triangular median and lateral apical white patches on 2nd to 6th tergites. Venter bright brown, darkening somewhat in median area; hairs dark brown, except for the apical pale fringes and variably on lateral parts of sternites. Genitalia with wide gonopophyses and truncate cerci.

Distribution.—QUEENSLAND: Brisbane, Nov., Hacker; Mt. Tamborine, Froggatt; Nerang, Oct. NEW SOUTH WALES: Kew, Jan.; Kendall, Nov.–Mar., Henry; Port Stephens; Lake Macquarie, Dec.; Galston, Jan., Wood; Sydney (Narrabeen), Jan., Feb., Burns, Wirth; Bundeena, Dec., Nikitin; National Park, Jan., Goldfinch, I.M.M., Nicholson. VICTORIA: Drummer Mt., Nov., Perkins; Cann R., Jan., Broome, Drummond; Lake Curlip, Feb., Dobrotworsky; Yarram, Mar., Douglas; Wilson's Promontory, Jan., Feb., Douglas, Nicholson.

MESOMYIA (LILAEA) NORRISI, sp. nov.

Type.—Holotype ♀, from Albany, W.A., 8.i.1935, K. R. Norris, in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Material examined.—10 ♀ ♀.

A medium-sized, parallel-sided, dark brown species; with long, flask-shaped, blackish brown callus; dark brown antennal plate; brown legs; and a somewhat variegated, dark brown abdomen, with prominent median and lateral apical triangles of white hairs on tergites. Length 12–14 mm.

Resembles *lurida* in general coloration and pattern, but distinguished by smaller size, less robust build, narrower frons, larger, differently shaped callus, and shape of gonopophyses. To be separated from *paralurida* by more hairy body, darker colour, darker callus, antennal plate, and legs, and shape of gonopophyses.

Female (Figs. 39, 47)

Head.—Frons relatively narrow, index about 3.5, with brown tomentum, short black hairs, and a greyish fawn line at eye margins; ocellar tubercle grey, with black and greyish cream hairs; callus blackish brown, flask-shaped, three-fourths width of frons at base, and tapering above to a point a little below ocellar tubercle. Subcallus dark brown, shining, surrounded by light fawn tomentum; parafacials and face light fawn-grey, with dark brown hairs on parafacials and white ones on face. *Antennae*: 1st and 2nd segments brown, with greyish tomentum and short black hairs; 3rd dark to blackish brown, somewhat paler at base and

sometimes on style. Palpi fawn-brown, with brighter brown lateral bare concavity, and white hairs on 1st segment, short black ones on 2nd. Beard white.

Thorax.—Scutum with blackish brown median and sublateral areas; dorsocentral vittae diffuse, greyish anteriorly, brownish posteriorly; lateral areas similar, with a darker brown mark above wing root; scutellum blackish brown centrally, brighter brown apically and laterally. Hairs on disc relatively long and woolly, as in *lurida*, mixed dull cream and brown; notopleural hairs mixed yellowish cream and dark brown; supra- and postalar tufts and lateral marginal scutellar hairs white, with some brown hairs above in postalar tuft. Pleura light fawn-grey to brownish, with long, relatively dense, whitish hairs, and some brown ones on upper mesopleural convexity.

Legs.—Brown, variably darker on femora, and darkening to blackish at lower ends of tibiae and on tarsi. Hairs predominantly white on mid and hind femora, black elsewhere.

Wings.—Faintly greyish; stigma brown, inconspicuous; veins brown.

Abdomen.—Dark brown, variably marked with black, with a general greyish bloom, and with fawn-brown apical margins and median and lateral triangles on tergites. Hairs black, except for conspicuous white median tufts on 2nd to 6th tergites, and white lateral zone, which expands inwards to form a basal triangle on 2nd tergite and apical triangles on 2nd to 6th. Venter light brown, with a greyish suffusion, and a broad, diffuse, dark brown median stripe; hairs white, except for a predominance of black in the darker median zone and on whole of 7th sternite. Hypopygium with gonopophyses narrower than in *lurida*, base of furca concave, and caudal ends of spermathecal ducts short.

Some specimens have the subcallus and most of 3rd antennal segment darker than described, and the hairs on parafacials and face are sometimes more diffusely mixed dark and white. The ♀ from Victoria has a relatively narrow frons and callus, and the 8th sternite more like that of *paralurida*, but the furca and caudal ends of spermathecal ducts as in *norrisi*. It is quite dark, with blackish antennal plate, and more like *norrisi* than *paralurida*, so it is included here provisionally.

Distribution.—WESTERN AUSTRALIA: Lake Gnangara, Feb., Norris; Mt. Helena, May, L. Wilson; W. shore of Lake Muir, Manjimup, Feb., Calaby; Pemberton, Feb., Calaby; Nornalup, Jan., Norris; Albany, Jan., Norris. VICTORIA: Grampians, Jan., Dobrotworsky (identification doubtful).

MESOMYIA (LILAEA) PARALURIDA (Ferguson & Henry)

* *Silvius paraluridus* Ferguson and Henry, 1920, p. 839. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney.

Mesomyia (Lilaea) paralurida (Ferguson and Henry). Mackerras 1955*b*, p. 606.

Material examined.—22 ♀♀.

Close to *lurida*, but smoother, less hairy, less broadly built, and further distinguished as noted below. Length 14–16 mm.

Female (Figs. 40, 48)

Head.—Frons narrower, index 3.5, and darker brown than in *lurida*, with the callus narrower and less conspicuous, but usually with an irregular, ridged,

triangular upward prolongation. Subcallus darker, and not as shining as in *lurida*; parafacials and face more greyish fawn; antennae darker brown.

Thorax.—Scutum more extensively dark greyish brown, with the dorsocentral lines widening markedly in front of scutellum, and the paler lateral areas relatively narrow. Pleura, legs, and wings as in *lurida*.

Abdomen.—Bright yellowish brown, with apices of tergites paler, and 3rd and subsequent tergites variably darkened in middle, at least 5th to 7th being predominantly dark brown; hairs black, with the median and lateral apical cream patches quite narrow and inconspicuous, not forming well-defined triangles as in *lurida*. Venter light yellowish brown, with dark brown hairs; apices of sternites paler, with cream hairs. Gonopophyses narrower and more projecting than in *lurida*; cerci longer, more rounded.

Distribution.—NEW SOUTH WALES: Cloud's Ck., Nymboidea R., Jan.; Macksville, Nov., Campbell; Kew, Jan.; Kendall, Nov.–Mar., Henry; Myall Lakes, Jan., Graham.

MESOMYIA (LILAEA) STRADBROKEI (Taylor)

* *Silvius stradbrokei* Taylor, 1917*b*, p. 519. Type ♀, from Stradbroke I., S. Qld., 5.xii.1913, H. Hacker, in the Queensland Museum, Brisbane.

Mesomyia (Lilaea) stradbrokei (Taylor). Mackerras 1955*b*, p. 606.

Material examined.—1 ♀.

A slender, bright brown species; with reddish brown scutum; and wings with a faint yellowish grey tint. Length 13 mm. This may be merely a small faded specimen of *paralurida*, which would fall as a synonym; but there are differences in the genitalia (Figs. 48 and 49), and I have left the two separate until more material is discovered.

Female (Figs. 41, 49)

Head.—Frons shaped as in *paralurida*, index 3.5, with reddish brown tomentum and black hairs; callus narrow, elongate, light brown. Subcallus bright brown, not very shining; parafacials with grey tomentum and cream hairs; face light reddish brown, with cream tomentum below and cream hairs. *Antennae*: 1st and 2nd segments brownish yellow, with brown hairs; 3rd bright, somewhat reddish brown. Palpi bright brown, with inconspicuous dark hairs and some cream ones at base. Beard cream.

Thorax.—Scutum bright reddish brown, with a dark median line, narrow, slightly paler dorsocentral lines, sublateral areas distinctly darkened, particularly in front of suture, and lateral areas light fawn; hairs mainly dark and inconspicuous on disc, brown on notopleural lobe, and cream behind the suture. Scutellum bright, slightly reddish brown, rubbed. Pleura light brown, with pale greyish overlay and cream and brown hairs.

Legs.—Coxae with light creamy grey tomentum and cream hairs; remaining segments bright yellowish brown, darkening somewhat on tarsi; hairs cream on femora, brown on remaining segments.

Wings.—Greyish, with a faint yellowish hue; veins light yellowish brown.

Abdomen.—Bright, slightly yellowish brown, with apices of tergites paler, and 5th and subsequent tergites darkened on the disc; hairs dark brown, except for cream ones forming indefinite median apical triangles and lateral patches on the tergites. Venter light brown, with dark hairs.

Distribution.—QUEENSLAND: Stradbroke I., Dec., Hacker.

Subgenus PERISILVIUS Enderlein

Perisilvius Enderlein, 1922, p. 344, 1925, p. 316; Oldroyd 1957, p. 213. Type species *Perisilvius nyassicus* Enderlein, 1925, Ethiopian, by original designation. No Australian synonymy.

The reasons for accepting *Perisilvius* in the Australasian region have been given earlier. It contains a somewhat heterogeneous collection of species in the Ethiopian region (Oldroyd 1957), and it is possible that the *Pseudotabanus*-like

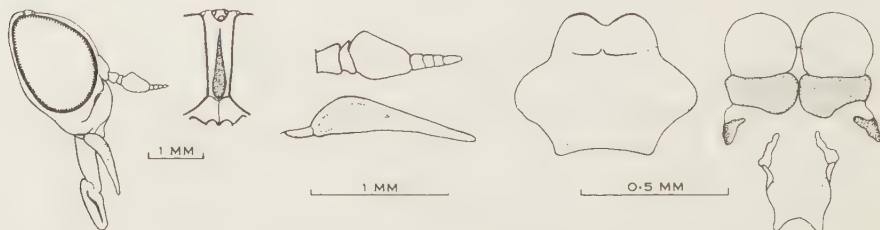


Fig. 50.—*Mesomyia (Perisilvius) demeijerei* (Ric.), ..

group which includes the Australasian species may need to be separated from the one containing the subgenotype. However, any subdivision should probably be based on an African rather than Australasian type species.

Female (Australasian species)

Relatively small (10–12 mm), smooth, light-coloured species, with clear wings. Eyes bare; unbanded. Frons converging, of medium width (index 3.5 or more), tomentose; callus narrower than frons at base, club-shaped, tapering smoothly. Subcallus, parafacials, and face entirely tomentose. First segment of antennae not expanded dorsally; 3rd with moderately broad basal plate and 4-annulate style. Palpi (Fig. 50) widened at base, and with well-defined lateral bare area. Hind tibial spurs moderately long, slender. Vein *sc* of wing bare. Genitalia undistinguished.

Male unknown.

In Australia, this subgenus can be separated from *Lilaea* by its small tomentose subcallus, from *Pseudotabanus* by the bare *sc*, and from both by shape of palpi and general habitus and coloration.

Only two species are at present included, *vittata* (Ric.) from New Guinea and *demeijerei* (Ric.) from New Guinea and Australia. Of the 7 other species from New Guinea and Celebes described as "*Silvius*" by Schuurmans Stekhoven

(1926, 1932), 6 are Diachlorini, and 1 (*atratus* Sch. Stk., 1926) may be a *Pseudotabanus*, as is an undescribed Papuan species that I have seen. Oldroyd (1947a) noted that van der Wulp and Ricardo had recorded that *vittata* had banded eyes; but he could detect no signs of a band on his specimens, and I have not been able to find any indications of one on eyes immersed overnight in Goffe's solution.

MESOMYIA (PERISILVIUS) DEMEIJEREI (Ricardo)

Silvius demeijerei Ricardo, 1913b, p. 405; Surcouf 1921, p. 142; Schuurmans Stekhoven 1926, p. 52 (misspelt *de Meyeri*). Type ♀, from New Guinea, in the Natura Artis Magistra Museum, Amsterdam. Paratypes in the British Museum (Natural History) agree well with specimens of *fulvohirtus* Taylor from Queensland.

Lilaea demeijerei (Ricardo). Oldroyd 1947a, p. 141.

Mesomyia (Pseudotabanus) demeijerei (Ricardo). Mackerras 1955b, p. 607, 1956a, p. 388.

* *Silvius fulvohirtus* Taylor, 1916, p. 814; Ferguson and Hill 1922, p. 251. Type ♀, from Townsville, N. Qld., 7.i.1914, F. H. Taylor, in the School of Public Health and Tropical Medicine, University of Sydney.

* *Silvius vicinus* Taylor, 1919, p. 46; Ferguson and Hill 1922, p. 251 (syn. of *fulvohirtus* Taylor). Type ♀, from Stradbroke I., S. Qld., 5.xii.1913, H. Hacker, in the Queensland Museum, Brisbane.

Material examined.—9 ♀♀ from Australia, 20 ♀♀ from New Guinea.

A small to medium, yellowish fawn species; with brownish yellow legs; clear wings; and abdomen yellowish basally, darker brown banded distally. Length 10–12 mm.

Female (Fig. 50)

Head.—Eyes green, unbanded in life. Frons medium, index 3.5, with bright golden-fawn tomentum and short dark brown hairs; callus dark brown, elongate, about two-thirds width of frons at base, and tapering evenly to below anterior ocellus. Subcallus pale yellowish cream; parafacials and face creamy white, with fine white hairs. *Antennae*: 1st and 2nd segments yellowish cream, with mixed black and white hairs and a row of black hairs on distal edge of 2nd segment; 3rd bright orange, darker on style. Palpi yellowish cream, with short, inconspicuous, light brown hairs. Beard white.

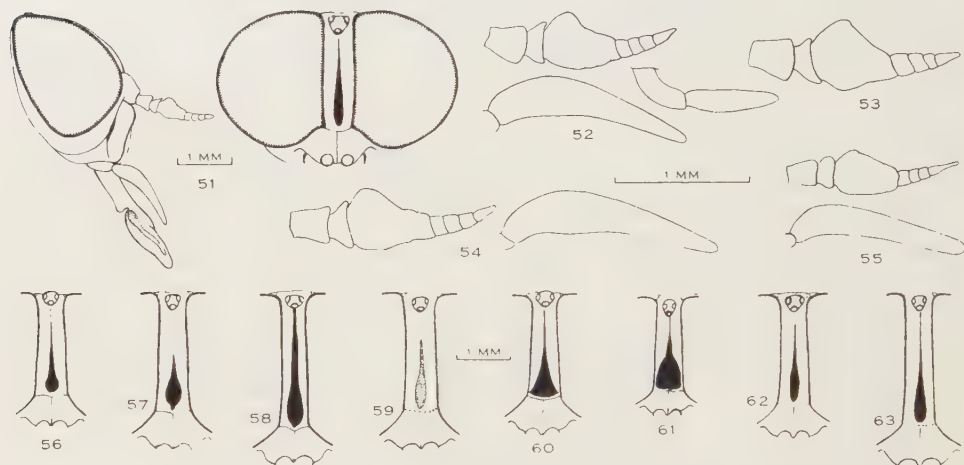
Thorax.—Scutum and scutellum almost uniformly covered with light olive-fawn tomentum and short yellowish cream hairs, which are longer and more conspicuous in front of and on scutellum. There are faint indications of median and dorsocentral lines, and the lateral areas are a little paler than the disc. Pleura ashy grey, with greyish white hairs.

Legs.—Femora brownish yellow, hind pair a little darker, the fore femora with mainly brown hairs, mid and hind with creamy white hairs; tibiae and tarsi darker, becoming dark brown on tarsi, and with dark brown hairs.

Wings.—Faintly greyish; stigma brown, well defined; veins brown: *R*₁ somewhat angulate, and with inconstant vestige of an appendix.

Abdomen.—First and 2nd tergites light brownish yellow, remainder more or less extensively suffused with dark brown; apical margins of 2nd to 5th or 6th with pale fawn-cream bands. Hairs mainly black on disc, pale yellowish cream on apical margins of 2nd or 3rd to 5th tergites and variably in mid-line; lateral hairs not especially dense, predominantly pale yellowish cream. Venter with 1st and 2nd sternites creamy yellow, remainder mainly dark brown, all with pale greyish cream apical bands; hairs creamy white on first 5 sternites, predominantly black on 6th and 7th.

Distribution.—QUEENSLAND: Moa I., Schomberg; Cape York (Jacky Jacky Ck.), May, M.J.M.; Cairns, Aug., Hull, Jarvis, Taylor; Townsville, Taylor; Stradbroke I., Dec., Hacker.



Figs. 51-63.—The *distincta* group of subgenus *Pseudotabanus*, ♀♀, except palps of ♂ in 52: 51, 54, 62, *distincta* Ric.; 52 and 56, *ater* (Tayl.); 53 and 59, *grandis* (Ric.); 55 and 61, *taylori*, nom. nov.; 57, *nigripennis* (Ric.); 58, *fergusoni* (Ric.); 60, *fuscipennis* (Ric.); 63, *queenslandi* Ric.

Subgenus PSEUDOTABANUS Ricardo

Pseudotabanus Ricardo, 1915c, p. 271; Surcouf 1921, p. 132; Enderlein 1925, p. 271; Ferguson 1926a, p. 301; Mackerras 1955b, p. 607. Type species *Pseudotabanus distinctus* Ricardo, 1915, north Queensland, by designation of Enderlein 1925, p. 271.

Veprilla Mackerras, 1955b, p. 603. Type species *Silvius frontalis* Ricardo, 1915, Northern Territory, by original designation. Examination of additional material has indicated that a better balance would be achieved by treating this segregate as a species group within the subgenus *Pseudotabanus* than by maintaining it as an independent subgenus.

Female

Large to small, smooth species. Eyes nearly always bare. Frons and callus differing in the groups. Subcallus and face tomentose. Basal plate of 3rd antennal segment sometimes with incipient subdivisions; style 4-annulate. Palpi of medium width to slender, firm, rounded apically, almost always without bare area. Proboscis strong. Hind tibial spurs variable, sometimes very small. Wing with

vein *sc* setulose, at least below. Genitalia dorsoventrally compressed, undistinguished.

Male

Sexual dimorphism often marked. Eyes bare; upper facets slightly to considerably enlarged. Genitalia of *distincta* and *lunulata* groups with the halves of the 9th tergite characteristically divided more or less completely into proximal and distal portions, and the style produced below into a projecting subapical ventral lobe, which is seen in dorsal view as an oval clear area (Figs. 22 and 23); those of *silvester* group (*silvester* only) with halves of 9th tergite not divided, and style without ventral lobe.

This is a striking subgenus in Australia, and it contains the species most commonly met with in the northern half of the continent. It is divided into three groups, which are so different that it will be convenient to treat them separately. They may be defined as follows:

distincta Group.—Relatively large (11–16 mm, few ♀♀ less than 12 mm), dark, ornate, strikingly *Cydistomyia*-like species. Eyes unbanded. Frons of ♀♀ narrow (index 3.5 or more), usually parallel to slightly diverging; callus (Figs. 56–63) fusiform or Indian club-shaped, usually narrower than frons at base. First antennal segment not expanded dorsally. Palpi (Figs. 51–55) usually tapering, *Cydistomyia*-like. Wings distinctly darkened, at least anteriorly. Sexual dimorphism marked, ♂♂ being smaller and more hairy than ♀♀, and having a characteristic abdominal pattern of yellowish basal and blackish apical tergites, or a black median vitta.

lunulata Group (= *Vepriella* Mack.).—Mostly small to medium-sized (9–12, occasionally 14 mm), undistinguished species. Eyes of ♀♀ with 2 oblique blue to green bands on a darker ground. Frons medium to rather narrow (index 3–4), usually parallel or converging; callus (Figs. 72–76) quadrate and full width of frons at base, with a narrow median extension to anterior ocellus. First antennal segment usually expanded, hood-like dorsally. Palpi long and slender. Wings usually clear. Sexual dimorphism not marked, but ♂♂ apparently have only 1 green band on eyes.

silvester Group.—Small (7–11 mm, few ♀♀ more than 10 mm), usually drab, narrow-bodied species. Eyes unbanded. Frons of ♀♀ wide (index 2–3), diverging to parallel, occasionally slightly converging; callus (Figs. 83–88) wider and more variable in shape than in *distincta* group, sometimes nearly full width of frons at base. First antennal segment not expanded dorsally. Palpi generally long and narrow. Wings usually clear. Sexual dimorphism (♂ of *silvester* only) moderate, not as great as in *distincta* group. As indicated earlier, I believe that this group evolved independently from ancestral *Mesomyia* stock, and I would treat it as a separate subgenus if I could find sufficient morphological reason to do so.

The distincta Group

This group contains eight rather striking species, which are comparatively easy to identify. Their distribution is shown in Figure 5.

KEY TO SPECIES OF THE *distincta* GROUP OF THE SUBGENUS PSEUDOTABANUS*Females*

1. Blackish species, with the wings largely or entirely suffused with dark brown to black2
Brown species, with the wings largely clear, or suffused with lighter brown4
2. Basal cells of wings clear; frons index 5. South Queensland, New South Wales
.....*fergusoni* (Ric.)
Basal cells of wings dark; frons index 3.53
3. Tip and posterior edge of wings pale; hairs on frons, parafacials, and face cream to white. North Queensland*nigripennis* (Ric.)
Tip and posterior edge of wings dark; hairs on frons and parafacials black, on face brown. Northern Territory*ater* (Tayl.)
4. A large (16 mm), broadly built species, with wings uniformly suffused with brown. North-western Australia*grandis* (Ric.)
Not such large (11–15 mm), less broadly built species; wings with at least some pale areas5
5. Wings brown, with discrete pale spots at apices of basal cells, fork of R_{4+5} , and apex of discal cell. North Queensland*fuscipennis* (Ric.)
Wings with more extensive clear areas, but no discrete spots in the situations indicated6
6. Callus more than half width of frons at base; wings irregularly clouded across middle and along veins; abdomen as in *distincta*. Northern Territory*taylori*, nom. nov.
Callus less than half width of frons at base; wings largely clear, with variable blackish suffusion in radial area. North Queensland7
7. Pale abdominal bands narrowest in middle, evenly curved, and widening laterally; frons index 3.5. Townsville to Rockhampton*distincta* Ric.
Pale abdominal bands produced in middle to form well-defined median triangles; frons index 4.5–5.5. Dunk I. to Cape York*queenslandi* Ric.

MESOMYIA (PSEUDOTABANUS) ATER (Taylor)

* *Silvius ater* Taylor, 1917a, p. 751 (Apr.), 1918, p. 63 (syn. of *nigripennis* Ricardo). Type ♀, from Brock's Ck., N.T., 19.i.1914, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney. Taylor sank his species in synonymy on the advice of the late E. E. Austen, but the differences between it and *nigripennis*, though small, are too evident, and appear to be too constant, to be ignored.

Mesomyia (Pseudotabanus) ater (Taylor). Mackerras 1955b, p. 607, fig. 14 G.

Material examined.—1 ♂, 8 ♀.

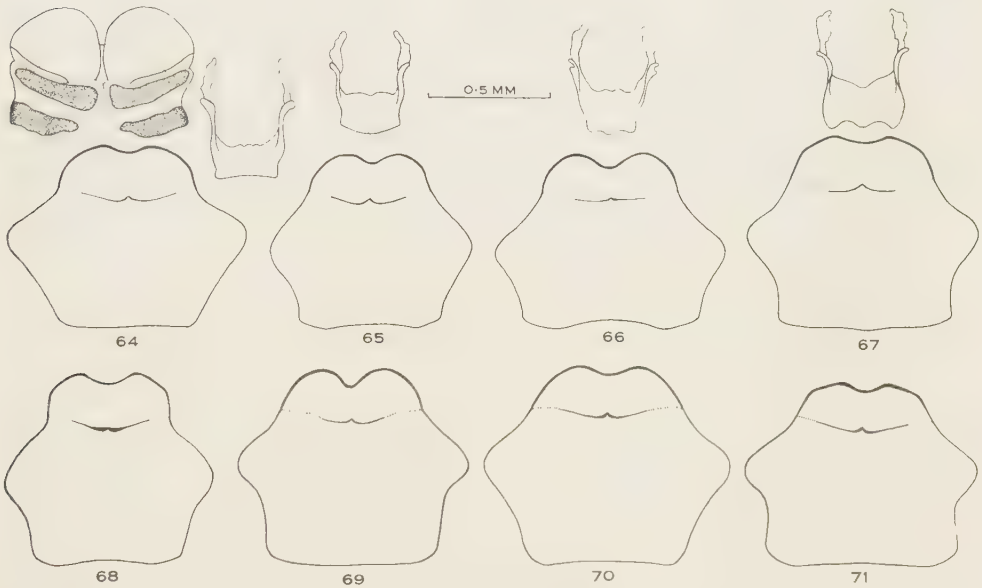
A robust black species; with almost uniformly blackish brown wings; and conspicuous white apical bands (interrupted or obscured in the middle) on the abdominal tergites. Length 12–14 mm.

Female (Figs. 52, 56, 64)

Head.—Frons parallel or slightly diverging, index 3.5, with light fawn to greyish tomentum, and a zone of short black hairs on almost the full length on each side; callus blackish, about one-third width of frons at base, narrowly club-shaped, tapering to a fine line extending almost to anterior ocellus. Subcallus cream to creamy grey, brown around antennal sockets and laterally, and with a group of short black hairs on each side lateral to antennae; parafacials greyish, with short

black hairs above, dull cream to whitish ones below; face with pale grey and brown tomentum, and a group of brown hairs on each side below antennae. *Antennae*: all segments blackish brown; 1st and 2nd with some overlying greyish tomentum and black hairs; 3rd showing indications of subdivision of the plate. Palpi dark to blackish brown, with short black hairs. Beard dull cream, with some admixture of darker hairs.

Thorax.—Scutum brownish black, with some overlying greyish tomentum anteriorly, through which indications of median and dorsocentral lines can sometimes be seen; lateral areas greyish; hairs black, mixed with some whitish ones



Figs. 64–71.—The *distincta* group of subgenus *Pseudotabanus*, ♀ genitalia: 64, *ater* (Tayl.); 65, *taylori*, nom. nov.; 66, *distincta* Ric.; 67, *queenslandi* Ric.; 68, *nigripennis* (Ric.); 69, *fergusoni* (Ric.); 70, *grandis* (Ric.); 71, *fuscipennis* (Ric.).

anteriorly and sublaterally; marginal hairs mainly blackish brown, with very small whitish tufts above and behind the wing root. Scutellum blackish brown, with some greyish overlay and black hairs. Pleura dark brown, with irregular grey overlay; hairs relatively sparse, dark brown to black, except for greyish white on proepimeron, propleura, lower part of mesopleura between coxae, a very small patch on the posterior edge of the upper mesopleural convexity, and just below and behind the wing root.

Legs.—Coxae brown, with greyish reflections and mainly dark brown hairs; remaining segments brownish black, with black hairs.

Wings.—Deep brown, almost blackish, but clear at extreme base and on a narrow strip between R_1 and R_s ; tip and posterior margin dark; veins dark brown.

Abdomen.—Black; 1st tergite grey along posterior margin and laterally; remaining tergites with pale grey apical margins, which widen laterally, and are inconspicuous, or interrupted by darker colour, in the median zone; hairs dark brown on the darker parts and on the median third of the apical edges, silvery white, conspicuous, on the lateral thirds apically. Sternites black, with black hairs, and conspicuous greyish white apical bands covered with silvery white hairs.

Male (Fig. 52)

Eyes large, contiguous; upper facets distinctly enlarged, three to four times as big as lower, and fairly clearly marked off from them. Subcallus, parafacials, and face dark to yellowish fawn, with brown to blackish hairs; beard brown. Scutum and scutellum blackish brown, with a little grey tomentum anteriorly, and with long, dense, deep brown hairs; pleura with dense, dull to dark brown hairs. Legs and wings as in ♀, anterior coxae somewhat greyish.

Abdomen with 1st and 2nd tergites creamy yellow, with golden hairs; 3rd yellow, irregularly marked with black across the middle (possibly a stain), and covered with golden hairs; subsequent tergites brownish black, paler on apical edges, and with black hairs. Venter similar to dorsum, but the darker colour on 3rd sternite seems more natural, and there are more dark than golden hairs on it. Genitalia brown.

Distribution.—NORTHERN TERRITORY: Brock's Ck., Dec., Jan., Feb., Campbell, Hill; Litchfield, Daly R., Jan., Campbell.

MESOMYIA (PSEUDOTABANUS) NIGRIPENNIS (Ricardo)

* *Silvius nigripennis* Ricardo, 1917, p. 213 (Feb.); Surcouf 1921, p. 143; Ferguson 1921b, p. 15. Type ♀, from Claudie R., N. Qld., J. A. Kershaw, in the National Museum, Melbourne. Not Taylor 1918, p. 63 (= *ater* Taylor).

Mesomyia (Pseudotabanus) nigripennis (Ricardo). Mackerras 1955b, p. 607, figs. 14 B, C.

* *Silvius nigroapicalis* Ferguson, 1921b, p. 15. Type ♂, from Claudie R., N. Qld., January, in the National Museum, Melbourne. A comparison with the degree of sexual dimorphism in other species of the group leaves no doubt that this is the ♂ of *nigripennis* Ricardo.

Material examined.—3 ♂♂, 4 ♀♀.

Close to *ater*, but differing as described below. Length 13–15 mm.

Female (Figs. 57, 68; Plate 1, Fig. 9)

Frons, subcallus, parafacials, and face fawn-cream, with creamy white hairs. Tufts of white hairs on scutum above and behind wing root more conspicuous, as are the sublateral white hairs above the black notopleural hairs. Pleura grey, with white to dull cream hairs, mixed with darker ones only on upper mesopleural convexity. Coxae grey, with predominantly white hairs. Wings with narrow clear zone at tip and extending along the posterior margin.

Male (Figs. 14, 22)

Eyes with upper facets only slightly enlarged, and not sharply differentiated from the lower. Subcallus, parafacials, and face with golden yellow tomentum

and hairs. Scutum with notopleural hairs deep brownish gold, the small tufts above and behind wing root pale gold. Pleura and coxae with dense, dull to brownish gold hairs; remainder of legs and wings as in ♀. Abdomen with 1st tergite blackish brown basally, yellowish apically; 2nd and 3rd entirely yellowish, with slightly paler apical edges and golden hairs; remaining tergites brownish black, with black hairs and their apical edges narrowly brown. Venter similar to dorsum.

Distribution.—QUEENSLAND: Claudie R., Jan., Feb., Kershaw.

MESOMYIA (PSEUDOTABANUS) GRANDIS (Ricardo)

* *Silvius grandis* Ricardo, 1917, p. 212; Taylor 1919, p. 46; Ferguson 1921a, p. 370; Surcouf 1921, p. 143. Type ♀, from Fortescue R., Hamersley Range, N.W.A., in the South Australian Museum, Adelaide.

Mesomyia (Pseudotabanus) grandis (Ricardo). Mackerras 1955b, p. 607.

Material examined.—1 ♂, 3 ♀.

A large dark brown species; with well-defined white apical bands on abdominal tergites; and almost uniformly brown wings. To be distinguished from *ater* by much lighter general coloration and uninterrupted pale abdominal bands. Length 16 mm.

Female (Figs. 53, 59, 70)

Head.—Frons parallel, index 3·5, with fawn-brown tomentum, and short white hairs on either side of the brown callus, which is of similar shape to that of *ater*. Subcallus, parafacials, and face pale greyish fawn, with dull cream hairs lateral to antennae and on parafacials, and white ones below antennae on face. *Antennae*: 1st segment grey on basal third, black on apical two-thirds, with black hairs; 2nd deep brown to black, with black hairs; 3rd brownish black. Palpi dark brown, with very short dark brown hairs on 2nd segment. Beard short and sparse, creamy yellow.

Thorax.—Scutum and scutellum uniformly brown, with indications of greyish dorsocentral vittae and lateral areas; hairs short, mixed inconspicuous dark brown and white; notopleural hairs dark brown, and small white tufts above and behind wing root as in related species. Pleura light brown, with some greyish overlay; hairs mainly creamy white, a group of dark brown ones on upper mesopleural convexity.

Legs.—Fore coxae pale grey, brownish apically, with white hairs, mid and hind brown, with dark brown hairs; remaining segments brown, with dark brown hairs showing paler reflections in certain lights.

Wings.—Almost uniformly medium brown with a faint greyish hue; the only indication of a paler area is between R_1 and R_s , and it is not very evident; veins light brown to somewhat yellowish brown distally.

Abdomen.—Brown; 1st tergite rather extensively grey apically and laterally; 2nd to 4th with indications of wide irregular dark median vitta, and with narrow but well-defined pale grey apical bands, which widen distinctly laterally; 5th and 6th entirely dark; hairs dark brown on the darker areas, silvery white, sparse, on

the apical pale bands. Venter banded like the dorsum, but the apical bands on the sternites are whiter.

Male

A single ♂ in the South Australian Museum, with same data as the ♀♀, probably belongs to this species. It is paler than the ♀, with creamy gold woolly hairs on scutum, darker brownish yellow hairs on notopleural lobes and upper part of pleura, and first 2 abdominal segments bright yellowish and covered with bright golden hairs; remainder of abdomen missing. Eyes with upper facets clearly enlarged, but not sharply separated from the smaller facets. Parafacials and face yellowish fawn, with creamy yellow hairs. Palpi dark brown, with blackish brown hairs.

Distribution.—WESTERN AUSTRALIA: Fortescue R., Hamersley Ra. (no other data). •

MESOMYIA (PSEUDOTABANUS) FUSCIPENNIS (Ricardo)

* *Silvius fuscipennis* Ricardo, 1917, p. 212; Surcouf 1921, p. 143; Ferguson 1926a, p. 304. Type ♂, from Cape York, ♀ from Claudie R., N. Qld., J. A. Kershaw, in the British Museum (Natural History).

Mesomyia (Pseudotabanus) fuscipennis (Ricardo). Mackerras 1955b, p. 607.

* *Veprius sexguttatus* Enderlein, 1925, p. 315; Ferguson 1926a, p. 304 (syn. of *fuscipennis* Ricardo). The type ♀, from "Nord Australien", in the Berlin Museum, was received through the kindness of Professor F. Peus, and Ferguson's synonymy confirmed.

Material examined.—1 ♂, 14 ♀♀.

A dark brown species; with brown wings, which are marked with conspicuous, clearer spots; and strongly banded abdomen. Length 12–16 mm.

Female (Figs. 60, 71; Plate 1, Fig. 11)

Head.—Frons parallel, index 3·5, with fawn-cream tomentum and short cream hairs; callus blackish brown, wedge-shaped, almost full width of frons at base. Subcallus, parafacials, and face light greyish fawn, with white hairs, except for a patch of short black ones lateral to antennae. Antennae black, the basal segments with a little greyish overlay and black hairs. Palpi deep to blackish brown, with very short dark brown hairs. Beard white, rather sparse.

Thorax.—Scutum and scutellum dark brown, with considerable greyish overlay laterally and anteriorly, which can be seen in certain lights to form fairly wide dorsocentral vittae; hairs on disc dull cream to yellowish, with some dark brown ones on disc of scutellum and a few dull golden ones towards its apex; lateral hairs mainly dark brown in front of wing root, creamy white above and behind it and on sides of scutellum. Pleura light grey, with greyish white hairs.

Legs.—Coxae similar to pleura; remaining segments deep to blackish brown, with black hairs.

Wings.—Brown, except for pale costal cell and base, the dark colour deepest beyond apices of basal cells and in radial area, and adorned with three series of conspicuous paler markings: one across apices of basal cells from fork of *Rs* to *Cu*₁; a small round spot covering fork of *R*₄₊₅; and a band across apex of discal

cell. The differences in intensity of the brown in different parts of the wing and the three paler markings give the wing a characteristic, somewhat mottled appearance. Stigma dark brown; veins brown to light brown.

Abdomen.—Tergites brown, 2nd to 4th with a wide, irregular, blackish brown median vitta, and subsequent tergites entirely dark brown on their basal three-fourths; all with quite broad pale grey apical bands, those on 3rd and subsequent tergites tending to widen laterally. Hairs dark brown on the darker area, creamy white on the pale bands, but more or less replaced by brown in median zone of 3rd and subsequent tergites; sublateral pale apical hairs sometimes golden rather than cream on 5th tergite, and entirely dark on subsequent tergites. Venter banded as dorsum, but 1st and 2nd sternites a lighter greyish brown, and no golden hairs on 5th. The abdominal markings lead through the *taylori* pattern to that characteristic of *distincta*.

Male

The following notes were made on the allotype in the British Museum. Eyes relatively small; upper facets not enlarged. Palpi normal. Wings as in ♀. Abdomen with 1st to 3rd tergites yellow, with fused median blackish spots, remaining tergites blackish, with very narrow paler apical edges to 4th and 5th; venter paler, with no dark median stripe, but 4th and subsequent sternites as corresponding tergites.

Distribution.—QUEENSLAND: Cape York, MacGillivray; Claudie R., Feb., Kershaw; Lockhart R., Flint; Silver Plains Stn., Jan., Wassell.

MESOMYIA (PSEUDOTABANUS) TAYLORI, nom. nov.

* *Silvius distinctus* Taylor, 1920, p. 165, 1926, p. 193; Ferguson and Hill 1922, p. 250; Ferguson 1926a, p. 301 (notes possibly preoccupied). Type ♀, from Bathurst I., N.T., -x.1916, G. F. Hill, in the South Australian Museum. Not *Pseudotabanus distinctus* Ricardo, 1915, north Queensland.

Mesomyia (Pseudotabanus) distincta (Taylor). Mackerras 1955b, p. 607 (notes homonymy).

Material examined.—17 ♀ ♀.

A large black species; with narrow frons; well-defined scutal vittae; dark markings, and from *distincta* in wing markings and shape of callus. Length 12–13 mm.

Female (Figs. 55, 61, 65; Plate 1, Fig. 6)

Head.—Frons parallel, index 4, with fawn and greyish tomentum; callus wide, flask-shaped at base, and with tapering extension towards ocelli. Subcallus grey, more yellowish around bases of antennae; parafacials and face greyish to fawn, with dull cream hairs. Antennae dark to blackish brown; 1st segment with some greyish tomentum, 2nd and extreme base of 3rd often somewhat paler; 1st and 2nd with dark brown hairs; some specimens show fairly evident indications of incipient subdivision of the plate. Palpi short and of unusual shape (Fig. 55), dark brown, with brown hairs. Beard rather sparse, dull cream, brownish at junction with parafacials.

Thorax and legs.—Similar to *fuscipennis*, but not so dark.

Wings.—Greyish, clearer in costal and basal cells, and suffused with brown along veins beyond and below basal cells, giving the wing an irregularly clouded appearance, which is different from that seen in other species; veins dark brown, except *M* and part of *Rs*, which are unpigmented.

Abdomen.—Tergites dark brown, with dark brown hairs; colour in the median zone a little darker, and produced posteriorly until it almost reaches the apices of the tergites, giving the appearance of a dark median vitta; pale cream, white-haired apical bands restricted to more or less lunulate markings on each side of mid-line. Venter similar to dorsum, but with 2nd sternite sometimes largely pale, and with the pale bands straight and conspicuous on 2nd to 4th sternites, disappearing on more distal sternites.

Distribution.—NORTHERN TERRITORY: Bathurst I., Oct., Hill (known only from the type series).

MESOMYIA (PSEUDOTABANUS) DISTINCTA Ricardo

* *Pseudotabanus distinctus* Ricardo, 1915c, p. 272; Surcouf 1921, p. 132; Enderlein 1925, p. 271; Ferguson 1926a, p. 301. Type ♀, from Inkerman, near Townsville, N. Qld., W. Stalker, in the British Museum (Natural History).

Mesomyia (Pseudotabanus) distincta Ricardo. Mackerras 1955b, p. 607, figs. 3 C, 14 D, E, F, H.

Material examined.—12 ♀♀.

A brown species; with blackish antennae, palpi, and legs; the distal part of the radial area of the wing darkened; and well-defined pale abdominal bands, which are narrowest in middle and widen laterally. Length 12–13 mm.

Female (Figs. 51, 54, 62, 66; Plate 1, Fig. 12)

Head.—Frons parallel, index 3·5, with cream to greyish white tomentum and inconspicuous white hairs; callus elongate, Indian club-shaped, about one-third width of frons at base, and with a tapering extension nearly to ocelli. Subcallus, parafacials, and face creamy to ashy white, with white hairs. Antennae dark to blackish brown; basal segments with ashy tomentum and black hairs. Palpi dark brown; 2nd segment with short inconspicuous brown hairs. Beard rather sparse, white.

Thorax.—Scutum dark brown, with some greyish overlay, more conspicuous on the dorsocentral vittae, which show up clearly in front of suture in certain lights; shoulders cream, lateral areas grey to cream; hairs brown, some whitish ones anteriorly, dull creamy yellow on the notopleural lobes, whitish above and behind wing root. Scutellum deep brown, with brown hairs on disc and dull cream marginal ones. Pleura pale fawn to greyish, with whitish to pale creamy yellow hairs.

Legs.—Coxae grey, with white to cream hairs; remaining segments dark to blackish brown; femora with brown hairs, which show up paler in certain lights, tibiae and tarsi with dark brown hairs.

Wings.—Greyish, with the radial area beyond fork of *Rs* more or less darkened; in some specimens this area is deep brown, but in others the colour is only just perceptible. Stigma dark brown; veins brown.

Abdomen.—Basal three-fourths of the tergites deep brown, black in median zone, with dark brown hairs; apical fourth greyish white, with white hairs, the pale colour narrowest in the median line and expanding laterally. The pale bands are clearly defined on all visible tergites. Venter similar to dorsum, except that 1st and 2nd sternites are almost entirely pale, and the pale bands on the others may widen in the middle.

Distribution.—QUEENSLAND: Magnetic I., Jan., O'Gower; Townsville, Feb., O'Gower; Ching Do, Taylor; Inkerman, Stalker; Bowen, Simson; Yeppoon, Sept., Goldfinch.

MESOMYIA (PSEUDOTABANUS) QUEENSLANDI Ricardo

* *Pseudotabanus queenslandi* Ricardo, 1915c, p. 272; Taylor 1920, p. 165; Surcouf 1921, p. 132; Enderlein 1925, p. 271. Type ♀, from Kuranda, N. Qld., F. P. Dodd, in the British Museum (Natural History).

Mesomyia (Pseudotabanus) queenslandi Ricardo. Mackerras 1955b, p. 607, 1956a, pl. 1, fig. 9.

* *Corizoneura kurandae* Taylor, 1917a, p. 748, 1920, p. 165 (syn. of *queenslandi* Ricardo); Surcouf 1921, p. 134. Type ♀, from Kuranda, N. Qld., F. P. Dodd, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—4 ♂♂, 56 ♀♀.

Close to *distincta*; but distinguished by a narrow frons, better-defined scutal vittae, and conspicuous median apical pale triangles on abdominal tergites. Length 11–15 mm.

Female (Figs. 63, 67)

Head.—Similar to *distincta*, but frons index 4.5, and the callus longer. Incipient subdivisions of basal plate of 3rd antennal segment sometimes more obvious in this species and *distincta* than in other members of the group.

Thorax.—Scutum brown, with some greyish overlay, and clearly defined broad grey dorsocentral vittae, which extend the full length of the scutum; median line brown, but the brown colour of the median area on either side of it more or less invaded by grey, especially anteriorly; shoulders and lateral areas cream to greyish; hairs brown on the darker parts, white on the grey areas, and mixed brown and white on the notopleural lobes, the white hairs on the disc particularly conspicuous in front of scutellum. Scutellum dark brown, with ashy grey margin; hairs on disc brown, marginal hairs creamy white. Pleura, legs, and wings as in *distincta*, but radial area usually less darkened.

Abdomen.—Brown, darkening apically, and with brownish black hairs; 1st tergite with a narrow grey apical margin, which widens a little in the centre and greatly at the sides; 2nd to 5th with the paler apical margins more yellowish and indefinite, except in the mid-line, where there are pale creamy grey, white-haired triangles produced forward for at least two-thirds the depth of the tergite, and at the lateral margins, where the pale, white-haired area is sharply produced towards the base of the tergites; the brown colour bordering the median triangles is darkened, which accentuates them still further. The appearance of the dorsum is thus quite different from that of *distincta*. Venter similar to dorsum, and differing from *distincta* in 2nd sternite being largely dark brown.

Two ♀ ♀ from Cape York, one without further data and the other from Blackgin Creek, differ from the typical form in being smaller (11–12 mm), lighter brown in general colour, and in having 1st and 2nd abdominal sternites almost entirely pale. While they appear superficially to be rather different, they can be regarded at most as variants of *queenslandi*.

Male

Four ♂ ♂ from Port Douglas in the South Australian Museum are presumed to belong to this species, as they come from within its range, and there are traces of pale triangles on the abdominal tergites. They are smaller (11–13 mm), darker, and more hairy than the ♀ ♀, with only a trace of paler scutal vittae, and a different abdominal pattern. Eyes with upper facets only slightly enlarged. Subcallus, parafacials, and face dull yellowish fawn, with concolorous hairs. Palpi black, with greyish overlay and mostly black hairs. Wings more extensively suffused with black than in ♀.

Abdomen bright yellowish brown, darkening on apical tergites; with narrow yellowish cream apical bands, which widen to form incipient median triangles; and an interrupted median black vitta, composed of oblong black spots, decreasing in size from 1st to 3rd tergites, forked on 4th, and merging into the darker ground colour on subsequent tergites. Hairs mainly black on disc (somewhat rubbed), mainly yellow on lateral margins. Venter bright brownish yellow, darkening on apical sternites, and with yellowish cream to greyish white apical margins to all sternites; hairs black on discs of 3rd and subsequent sternites, yellowish cream on all of 2nd and apical margins of others.

Distribution.—QUEENSLAND: Cape York (Blackgin Ck.), Sept., I.M.M.; Lockhart R., Flint; Port Douglas, Oct., Baldwin; Kuranda, Dodd; Cairns, Jarvis, Taylor; Gordonvale; Bramston Beach, Sept., Oct., biting, Elliott, M. & M.; Innisfail, Oct., biting, M.J.M.; Cowley, Nov., I.M.M.; Silkwood, Oct., biting, M.J.M.; Dunk I., Oct., Dec., McIndoe.

MESOMYIA (PSEUDOTABANUS) FERGUSONI (Ricardo)

**Silvius fergusonii* Ricardo, 1917, p. 214; Taylor 1918, p. 62; Ferguson and Henry 1920, p. 839; Ferguson 1920, p. 132; Surcouf 1921, p. 143. Type ♀, from Milson I. (misspelt "Nelson I."), Hawkesbury R., N.S.W., in the British Museum (Natural History).

Mesomyia (Pseudotabanus) fergusonii (Ricardo). Mackerras 1955*b*, p. 607, fig. 14 *A*.

Material examined.—2 ♂ ♂, 20 ♀ ♀.

A large black species, with narrow frons; well-defined scutal vittae; dark brown wings, which are clearer in basal cells; and apical pale bands on 1st and 2nd abdominal tergites wider than on subsequent tergites. Length 14–16 mm.

Female (Figs. 58, 69; Plate 1, Fig. 10)

Head.—Frons narrow, index 5, grey to greyish white, more or less suffused with brown towards the brown ocellar tubercle; callus deep brown, elongate, more or less ridged. Subcallus, parafacials, and face greyish to creamy white, with mainly white hairs, including a patch on subcallus lateral to antennae. *Antennae*: 1st and 2nd segments brown, with variable greyish overlay and dark brown hairs; 3rd deep to blackish brown. Palpi dark brown, with dark brown hairs. Beard white.

Thorax.—Scutum and scutellum dark brown, with grey overlay anteriorly and variably in the median area, so that the grey dorsocentral vittae are sometimes well defined on their lateral sides only, and sometimes tend to disappear behind suture; lateral areas grey, shoulders and notopleural lobes light fawn. Hairs on disc greyish white appressed and dark brown erect; notopleural hairs pale above, black below, forming a dark zone between scutum and pleura; supra- and postalar tufts white; marginal scutellar hairs mixed greyish white and brown. Pleura grey, with dull cream hairs, except for rather conspicuous whitish zones below wing root and above posterior spiracle.

Legs.—Coxae grey, with dull cream to greyish white hairs; remaining segments deep to blackish brown, with dark brown to black hairs.

Wings.—Extensively suffused with brown, darker in radial area, and markedly paler at base and in both basal cells. Stigma dark brown; veins brown, the portion of *M* separating the basal cells weakly pigmented.

Abdomen.—Blackish brown, with dark brown hairs; 1st and 2nd tergites with wide, pale grey, white-haired apical bands, which widen somewhat in median line and laterally; 3rd and 4th with narrower pale bands, which are more or less replaced by brown in median zone, and tend to disappear on 5th and subsequent tergites. Venter similar to dorsum, except that the apical bands on 2nd to 4th sternites are wider and of more uniform width, and the zone of white hairs tends to extend beyond their basal margins.

Male

Eyes with upper facets only slightly enlarged. Subcallus, parafacials, and face light creamy fawn, with cream hairs. Palpi brown. Pleura and coxae grey, predominantly with cream hairs, but with a dark brown patch on the posterior part of the upper mesopleural convexity.

Abdomen with 1st tergite blackish brown at base, brownish yellow and with golden hairs apically and laterally; 2nd brown, with pale creamy yellow apical margin, an incomplete brownish black median vitta, and black hairs except for a golden fringe on apical edge; 3rd brown, with the median darker vitta more obscure, hairs black on disc, dull golden along apical edge, and bright creamy gold on sublateral apical pale areas; remaining tergites brownish black, with black hairs, 4th with a dull golden apical fringe. Venter similar to dorsum, with greyish white apical bands on 2nd to 4th sternites wide and conspicuous, and only a trace of a median darker vitta.

Distribution.—QUEENSLAND: Fraser I., Feb., M.J.M.; Coolum, Mar., G.L. NEW SOUTH WALES: Richmond R.; Kew, Jan.; Kendall, Nov.–Mar., Henry; Toronto, Filmer; Milson I., Hawkesbury R.; Peat's Ferry, Hawkesbury R., Dec., Carter.

The lunulata Group

This group contains three rather distinctive species, and a series of variable sympatric populations in the Northern Territory (Fig. 7). These have been difficult to classify, and I have been able to recognize only two reasonably differentiated

species among them. The female genitalia have been of little assistance in discriminating between them.

KEY TO SPECIES OF THE *lunulata* GROUP OF THE SUBGENUS PSEUDOTABANUS

Females

1. Blackish to dark chocolate brown species; 1st antennal segment not expanded dorsally2
Bright brown to yellowish or greyish species; 1st antennal segment more or less expanded.
hood-like dorsally3
2. A larger (12–13 mm), broader, more hairy, blackish brown species, with median triangles
of white hairs on abdominal tergites. Eastern New South Wales*pulla*, sp. nov.
A smaller (10–11 mm), more slender, smooth, chocolate brown species, with narrow
but conspicuous apical white bands on abdominal tergites. Northern Australia
.....*equina* (Ferg. & Hill)
3. Abdomen predominantly yellowish to reddish brown, sometimes darker, and sometimes
concolorous, but usually with creamy yellow to greyish white apical margins and
median triangles which point forward from apices of tergites; subcallus with, at most,
inconspicuous hairs lateral to antennae. Northern and south-western Australia
.....*lunulata* (Big.)
Abdomen predominantly greyish, with conspicuous dark brown median triangles pointing
posteriorly from bases of tergites (reverse of *lunulata* pattern)4
4. A small (8–10 mm), brownish species; subcallus with hairs on whole length; 3rd antennal
segment short and wide (Fig. 73). Northern Territory*frontalis* (Ric.)
A relatively large (14 mm), more greyish species; subcallus without hairs; 3rd antennal
segment slender (Fig. 74). North Queensland*burnsi*, sp. nov.

MESOMYIA (PSEUDOTABANUS) LUNULATA (Bigot)

* *Tabanus lunulatus* Bigot, 1892, p. 688; Surcouf 1921, p. 74. Type ♀, from Australia, in the British Museum (Natural History). The type is in poor condition, but it agrees closely with the *insularis* form of this species.

Silvius lunulatus (Bigot). Ricardo 1915c, p. 259.

Mesomyia (?*Vepriella*) *lunulata* (Bigot). Mackerras 1955b, p. 603.

* *Silvius indistinctus* Ricardo, 1915c, p. 262, 1917, p. 217; Taylor 1916, p. 808, 1917a, p. 753; Ferguson and Hill 1920, p. 461; Ferguson 1921a, p. 368; Surcouf 1921, p. 143; Enderlein 1925, p. 314. Type ♀, from Adelaide R., N.T., in the British Museum (Natural History).

Mesomyia (*Vepriella*) *indistincta* (Ricardo). Mackerras 1955b, p. 603, fig. 11 (genitalia of both sexes, the ♀ wrongly cited as *frontalis* Ric.).

* *Silvius hilli* Taylor, 1916, p. 806; Ferguson and Hill 1920, p. 461 (syn. of *indistinctus* Ricardo). Type ♀, from Howard Ck., N.T., 18.viii.1913, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

* *Silvius borealis* Taylor, 1916, p. 809; Ferguson and Hill 1920, p. 461 (syn. of *indistinctus* Ricardo). Type ♀, from Howard Ck., N.T., 18.viii.1913, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

* *Silvius insularis* Ricardo, 1917, p. 216; Ferguson 1921a, p. 368; Surcouf 1921, p. 143. Type ♀, from Bathurst I., N.T., in the South Australian Museum, Adelaide.

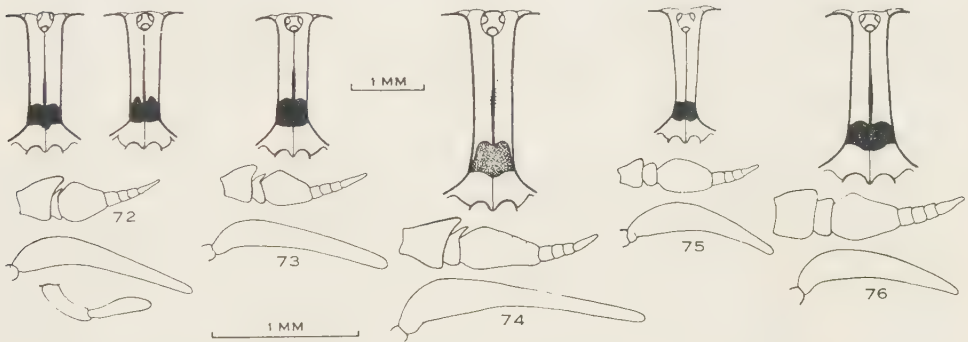
Mesomyia (*Vepriella*) *insularis* (Ricardo). Mackerras 1955b, p. 603.

Material examined.—2 ♂♂, 70 ♀♀.

A variable, usually light yellowish to reddish brown species; with light brownish yellow legs; clear wings; and usually paler median triangles on the abdominal tergites. Length 9–12 mm. The commoner form will be described first.

Female (Figs. 72, 77, 78)

Head.—Frons parallel or slightly converging, index 3·5–4, with brownish fawn tomentum and inconspicuous brown hairs; callus brownish black, with narrow extension. Subcallus, parafacials, and face with light creamy fawn tomentum and pale cream hairs, an inconstant group on subcallus lateral to antennae sometimes a little darker. *Antennae*: 1st and 2nd segments creamy fawn, with short black hairs, which are dense on the usually large dorsal prolongation of 1st segment; 3rd bright brownish orange. Palpi light brownish yellow, 1st segment with cream hairs, 2nd with short brown hairs. Beard light cream.



Figs. 72–76.—The *lunulata* group of subgenus *Pseudotabanus*, ♀♀, except palp of ♂ in 72: 72, *lunulata* (Big.), showing variation in frons; 73, *frontalis* (Ric.); 74, *burnsi*, sp. nov.; 75, *equina* (Ferg. & Hill); 76, *pulla*, sp. nov.

Thorax.—Scutum and scutellum bright, somewhat reddish brown, with the dorsocentral vittae and lateral areas a little paler, but inconspicuous; with dull cream hairs, except for the scutal-scutellar junction and central part of the disc of the scutellum, where the hairs are dark brown, and some brown hairs among the paler ones on the notopleural lobes. Pleura light fawn-grey, with creamy white hairs, mixed with some brown ones on upper mesopleural convexity.

Legs.—Coxae similar to pleura; remaining segments light brownish yellow to creamy yellow, with cream hairs on mid and hind femora, and mostly brown elsewhere; hind tibial spurs short, inconspicuous.

Wings.—Faintly greyish; stigma inconspicuous; veins pale yellowish brown anteriorly, brighter brown posteriorly.

Abdomen.—Variable; light yellowish brown, irregularly darkened on basal parts of tergites, and with their apical margins usually light yellowish fawn to greyish; hairs brown, with a variable number of pale cream ones on apical edges; there are often pale, cream-haired median and sometimes lateral apical triangles. Venter light brownish yellow, with fawn to greyish apical margins to the sternites;

first 6 with creamy white hairs, 7th (and sometimes median zone of 6th) with brown hairs. Genitalia with gonopophyses relatively wide, cerci rounded.

Male (Figs. 15, 23, 72)

Two ♂♂ from south-western Western Australia are presumably this species, although they were collected a long way from its principal habitat.

Eyes large, wider than thorax; meeting in mid-line; upper facets moderately enlarged, dark reddish brown, paler below, sharply marked off from the small, black, lower and posterior facets, which extend in a relatively broad zone to the occiput; a single bright green transverse band (in relaxed specimens) across upper half of lower small facets. Ocellar tubercle prominent, blackish; frontal triangle brown; subcallus small, pouting, fawn-cream, with brown hairs lateral to antennae; parafacials and face a little paler, with white hairs. Antennae more slender than in ♀: light yellow, darker on distal part of plate and style; basal segments with short black and light brown hairs, including a dense black tuft on the dorsal prolongation of 1st segment. Palpi brownish yellow, with mixed white and dark brown hairs. Vein R_1 of wing with oblique basal section and short appendix on both sides. Hind tibial spurs short, black.

This species is extremely variable, and 4 principal forms may be recognized.

The *hilli* form is larger (10–12 mm), yellowish to bright brown in general coloration, and has fairly well defined cream to yellowish cream apical triangles on the abdominal tergites. The dorsal expansion of 1st antennal segment is large (Fig. 72), the legs almost uniformly light brownish yellow, the venter with apical margins not much paler than ground colour, and 8th sternite as in Figure 78.

The *indistincta* (= *borealis*) form tends to be a little smaller (10–11 mm), and the abdomen is almost completely concolorous yellowish to dull brown, although the apical parts of the tergites may be vaguely paler; it agrees in other respects with the *hilli* form, and there is every gradation between the two.

The *lunulata* (= *insularis*) form is small (9–10 mm) and dark, like *frontalis*, but with clearly defined pale apical margins and white-haired median triangles, which tend to fuse into an irregular pale vitta, on the abdominal tergites. The frons is often relatively narrow (right-hand specimen in Fig. 72); 1st antennal segment moderately expanded; femora and apices of fore and hind tibiae distinctly darker than rest of legs; venter strongly fasciate; and gonopophyses (Fig. 77) relatively narrow, but wider than in *frontalis*. This is the most distinctive race; only 7 ♀♀ have been seen, and their distribution is noted below.

The south-western form, represented by 2 ♂♂ and 1 ♀ from the vicinity of Perth, is like the *hilli* form in having yellowish cream triangles on the abdominal tergites and widely separated gonopophyses; but it is more reddish brown in general colour, has more conspicuous brown (rather than cream) hairs on the subcallus lateral to the antennae, the 1st antennal segment of the ♀ (though not of the ♂♂) less expanded dorsally, and the venter strongly fasciate. It thus tends to bridge the gap between the *hilli* and *insularis* forms.

Distribution.—NORTHERN TERRITORY: Victoria R., Sept., Oct.; "Victoria River Downs", Mulhearn; Melville I., W. D. Dodd; Bathurst I. (*lunulata* form); Darwin, Sept., Jan., Hill; 30 miles E. of Darwin, Hill; Howard Ck., Hill; Darwin R., Sept., Campbell; Mt. Bundy, Sept., Campbell; Batchelor, Hill; 40 miles W. of Stapleton, Oct., Hill (*lunulata* form); Stewart Highway (60-mile post), Aug., Crawford (*lunulata* form); Adelaide R.; Brock's Ck., Aug., Sept., Campbell; Mt. Douglas and Mackinlay R., near Burrundie, Aug., on buffalo, Campbell, I.M.M.; Burrundie, Aug., I.M.M.; "Manbulloo", near Katherine, Oct., Bearup and Black. QUEENSLAND: Turn-off Lagoon, Sept., Campbell; Coen R. (Ricardo 1917). WESTERN AUSTRALIA: Yanchep, 32 miles N. of Perth, Jan., R. E. Turner (British Museum); Perth (Crawley), Dec., Norris; Rottnest I., Jan.

MESOMYIA (PSEUDOTABANUS) FRONTALIS (Ricardo)

Silvius frontalis Ricardo, 1915c, p. 262; Taylor 1917a, p. 753; Ferguson 1921a, p. 371; Surcouf 1921, p. 143; Enderlein 1925, p. 314. Type ♀, from Darwin, N.T., -xi.1908, stated to be in the German Entomological Museum. A paratype in the British Museum (Natural History) agrees with specimens from Australian collections.

Mesomyia (Vepriella) frontalis (Ricardo). Mackerras 1955b, p. 603, fig. 11, except ♂ and ♀ genitalia.

Material examined.—67 ♀ ♀.

A small brown species; with brown hairs extending to the top of the subcallus on each side; and with the basal brown bands on the abdominal tergites produced posteriorly to form dark median triangles and smaller lateral expansions. Length 8–10 mm.

Female (Figs. 73, 79; Plate 1, Fig. 5)

Head.—Frons parallel or slightly converging, index 3, with brownish fawn tomentum and short brown hairs; callus blackish brown, with narrow extension. Subcallus with fawn tomentum showing some greyish reflections, and with conspicuous brown hairs over its full length; parafacials and face pale greyish fawn, with white hairs. *Antennae*: 1st and 2nd segments with greyish tomentum and rather dense black hairs, especially on apical prolongation of 1st; 3rd uniformly brown. Palpi dull brown; 1st segment with cream hairs, 2nd with short dark brown hairs. Beard greyish white.

Thorax.—Scutum and scutellum brown, with greyish overlay on dorsocentral vittae and lateral areas; hairs mixed inconspicuous dark brown and more evident greyish white. Pleura light grey, with a brownish hue and greyish white hairs, mixed with some brown ones on upper mesopleural convexity.

Legs.—Coxae darker grey than pleura, with greyish white hairs. Femora brown with greyish overlay basally, becoming yellowish near apices; fore pair with mainly brown hairs, mid and hind with greyish white hairs. Tibiae yellowish brown basally, becoming darker distally, with brown hairs distally on fore pair, greyish white ones basally on fore pair and on all of mid and hind; tarsi brown, with dark brown hairs.

Wings.—Faintly greyish; stigma inconspicuous; veins yellowish brown anteriorly, brown posteriorly.

Abdomen.—Banded with dark brown on the basal half or less of the tergites, brownish grey apically, the relative extent of the light and dark colour (Plate 1, Fig. 5) being almost reversed from that usually seen. The brown bands on 2nd to 4th tergites are darkened in the median line, and prolonged into triangles which almost reach the apices of the tergites; they are also produced posteriorly at the lateral margins. The visible parts of 5th and 6th tergites are almost entirely brownish grey, with a median brown vitta, and brownish marks basally at the lateral margins; 7th entirely brownish grey. Hairs dark brown on both darker and paler areas, except for narrow greyish white apical fringes on the tergites. Venter brownish grey, darkening towards bases of sternites, and with dark brown hairs mixed with some greyish white ones; apices of sternites paler and with a greyish white fringe. Genitalia with gonopophyses narrow, cerci triangular.

Distribution.—NORTHERN TERRITORY: Darwin, Nov., Hill, Hunt; 30 miles E. of Darwin, Hill; Howard Ck., Hill; 34 miles S. of Darwin, Hill; Marrakai, July, Campbell, I.M.M.; Darwin R., Aug., Sept., Campbell; Batchelor, Hill; Brock's Ck., Aug., Campbell; Grove Hill, July, I.M.M.; Mackinlay R., near Burrundie, Aug., on buffalo, Campbell, I.M.M.; Larrimah, Sept., Bearup and Black; Groote Eyelandt, Tindale.

MESOMYIA (PSEUDOTABANUS) BURNSI, sp. nov.

Type.—Holotype ♀, from Koah, N. Qld., 18.x.1925, A. N. Burns, in the National Museum, Melbourne.

Material examined.—1 ♀.

Close to *frontalis*, from which it is distinguished by much larger size; paler, more greyish general coloration; slender 3rd antennal segment; reduced brown ground colour on scutum and abdomen; and differently shaped gonopophyses and cerci. Length 14 mm.

Female (Figs. 74, 80)

Head.—Eyes (not relaxed) with traces of the normal two bands. Frons slightly converging, index 4, with brown tomentum on upper two-thirds, light fawn below and at eye margins; callus bright brown, with somewhat darker, almost linear extension. Subcallus pale fawn-cream, with some short brown hairs lateral to antennae; parafacials and face cream, with mixed brown and creamy white hairs. *Antennae*: 1st and 2nd segments with light fawn-cream tomentum and brown and black hairs, the black especially concentrated in a dense tuft on the dorsal prolongation of 1st segment; 3rd reddish brown, paler at base and a little darker on style. Palpi light fawn-brown, with creamy white hairs on 1st segment, short brown ones on 2nd. Beard white.

Thorax.—Scutum brown, darker in median line and lateral to dorsocentral vittae, which are well defined, pale grey, and widen considerably behind suture; lateral areas light brownish grey; hairs on disc mixed brown erect and creamy white appressed; marginal hairs not dense, dark brown and dull cream on notopleural lobes, creamy white above and behind wing root. Scutellum pale grey basally and laterally, light brown in middle, with dark brown hairs in central area, creamy white ones laterally. Pleura pale grey, darker below, with creamy white hairs, and with a fawn tint and some brown hairs on upper mesopleural convexity.

Legs.—Coxae grey, with creamy white hairs; remaining segments bright, somewhat yellowish brown, a little paler at apices of femora and basally on tibiae; hairs predominantly creamy white on femora, brown elsewhere.

Wings.—Greyish, vaguely darker in costal cell and along some of the veins; stigma brown, elongate; veins brown; R_1 with angulated basal section and well-defined appendix.

Abdomen.—Grey, with brown basal bands widening laterally on 2nd and subsequent tergites, and with darker brown median spots or triangles, which almost reach posterior margins of 1st to 6th tergites, and decrease in size posteriorly; hairs dark brown on centre of 1st tergite and almost whole of discs of remainder, creamy white sublaterally and laterally on 1st tergite and on narrow pale apical edges and most of lateral margins of remaining tergites. Venter brown, with grey reflections, and pale apical margins to all sternites; hairs creamy white, mixed with dark brown in median zone, and with a strong, dark brown tuft on 7th sternite. Genitalia with wide gonopophyses and rounded cerci, more like those of *lunulata* than of *frontalis*.

Distribution.—QUEENSLAND: Koah, Oct., Burns.

MESOMYIA (PSEUDOTABANUS) EQUINA (Ferguson & Hill)

Silvius equinus Ferguson and Hill, 1922, p. 249, figs. 1 and 2. Type ♀, from Gordonvale, N. Qld., December, A. P. Dodd, was stated to be in the Australian Institute of Tropical Medicine, Townsville. This collection was transferred to the School of Public Health and Tropical Medicine, University of Sydney, but the type of *equinus* cannot be found, although others recorded as being in the Institute are present. The specimens I have seen differ from the original description in having a somewhat darker frons, and silvery rather than golden tomentum on occiput. Nevertheless, I believe that they belong to the same species, and I therefore select a ♀, from Turtle Ck., between Cairns and Port Douglas, N. Qld., 19.viii.1955, I. M. Mackerras, as neotype.

Mesomyia (Vepriella) equina (Ferguson and Hill). Mackerras 1955b, p. 603.

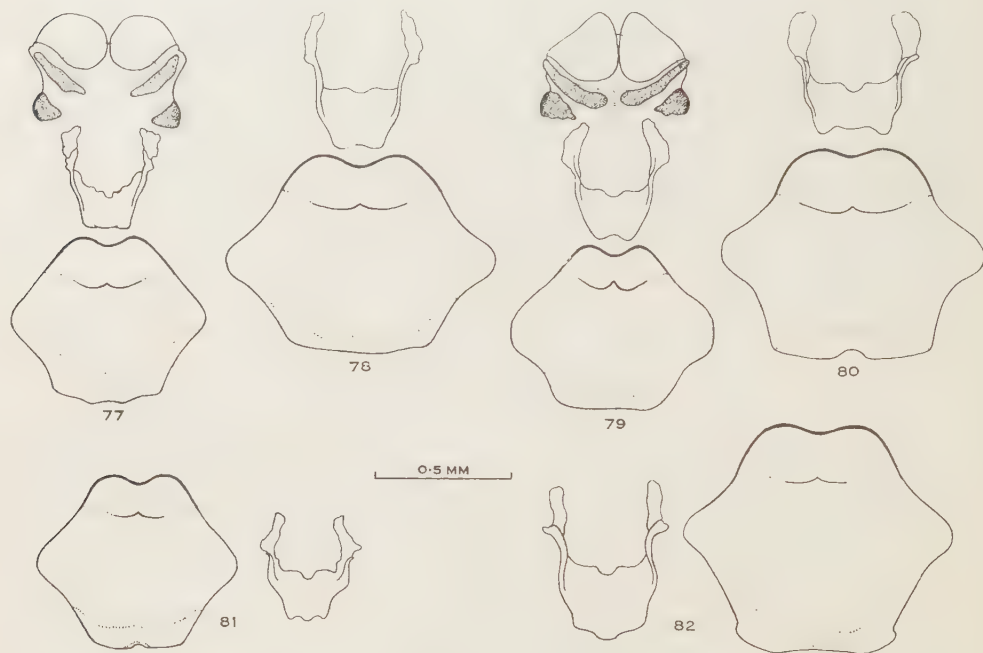
Material examined.—4 ♀ ♀.

A slender dark chocolate brown species; with brown legs; somewhat darkened wings; and narrow, almost straight, apical white bands on abdominal tergites. Length 11–12 mm.

Female (Figs. 75, 81)

Head.—Eyes brown in life, with 2 conspicuous oblique green bands. Frons converging, index 4.5, with brownish to brownish golden tomentum and short dark brown hairs; callus black, irregular on its upper margin, and produced into a narrow, black extension. Subcallus, parafacials, and face fawn to greyish; subcallus with variable, very short, inconspicuous brownish hairs at sides of antennae; parafacials and face with fine dark hairs, contrasting with the pale hairs on these areas in the preceding species. *Antennae*: 1st and 2nd segments with greyish fawn tomentum and black hairs; 3rd brown. Palpi dark brown, with short black hairs. Beard brown, rather sparse.

Thorax.—Scutum dark brown, irregularly marked with lighter brown, and with paler dorsocentral vittae and lateral areas, becoming vague behind suture. Hairs mixed dark brown and dull cream anteriorly, more creamy white posteriorly, especially in front of scutellum; marginal hairs dark brown in front of wing root, mixed brown and cream behind it. Scutellum a paler, more greyish brown than scutum, with some dark hairs basally, creamy white ones over most of its area and on margins. Pleura rather dark greyish brown, with brown hairs.



Figs. 77–82.—The *lunulata* group of subgenus *Pseudotabanus*, ♀ genitalia: 77 and 78, *lunulata* (Big.), showing range of variation; 79, *frontalis* (Ric.); 80, *burnsi*, sp. nov.; 81, *equina* (Ferg. & Hill); 82, *pulla*, sp. nov.

Legs.—All segments medium to deep brown, paler on knees and basally on fore and mid tibiae; hairs dark brown.

Wings.—Lightly suffused with brown, somewhat darker anteriorly and across apices of basal cells; veins brown to dark brown; R_4 somewhat angulate, and sometimes with vestige of an appendix.

Abdomen.—Deep chocolate brown, with dark brown hairs, and with narrow, almost straight, pale grey, white-haired apical bands on all visible tergites, except 6th, which has a pale margin but dark hairs, and 7th, which is entirely dark; the neotype also has incipient median apical white-haired triangles. Venter similar to dorsum. Genitalia as in Figure 81, cerci rounded.

Distribution.—NORTH-WESTERN AUSTRALIA: Brooking Gorge, Fitzroy R., Sept., Lukins (specimen greasy, identification not certain). QUEENSLAND: Turtle Ck., near Port Douglas, Aug., I.M.M.; Gordonvale, Dec., Dodd (Ferguson and Hill 1922); Yeppoon, Nov., Goldfinch.

MESOMYIA (PSEUDOTABANUS) PULLA, sp. nov.

Types.—Holotype ♀ and allotype ♂, from Blackheath, N.S.W., 14.i.1922, E. W. Ferguson, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—3 ♂♂, 4 ♀♀.

A medium-sized, rather hairy, blackish brown species; with light greyish brown wings; and narrow pale apical bands produced into small median triangles on the abdominal tergites. Length 12–13 mm.

Female (Figs. 76, 82)

Head.—Eyes with short, rather sparse, inconspicuous hairs; noted by Ferguson as “dark purple, with 2 blue-green transverse bars” in life. Frons slightly diverging, index 4, with brown tomentum, which shows darker in certain lights; callus black, normally quadrate below, and with rather irregular extension. Subcallus brownish fawn, without hairs; parafacials fawn along eyes, greyish medially, with brown and some pale hairs; face with light grey tomentum, more yellowish fawn on either side of the median area, and with some brown hairs below and lateral to antennae and a denser zone at sides. *Antennae*: 1st and 2nd segments with grey tomentum and black hairs, 1st large, but not produced dorsally; 3rd deep brown, paler at base, and becoming blackish on style. Palpi dark brown, with short black hairs. Beard mainly brown, but with mixture of some grey hairs posteriorly.

Thorax.—Scutum and scutellum dark brown, with grey dorsocentral vittae which fade behind suture, and with lighter brown lateral areas; hairs mainly blackish on disc, mixed with some dull creamy grey ones sublaterally and posteriorly; marginal hairs on scutum and scutellum mainly brown. Pleura brownish grey, with mostly brown hairs, but some paler ones anteriorly and below posterior spiracle.

Legs.—Coxae greyish brown, with greyish white and brown hairs; femora deep brown, with dark brown hairs on fore pair, mostly cream on mid and hind; tibiae and tarsi brighter brown, with dark brown hairs.

Wings.—Light greyish brown, costal cell a little darkened; stigma and veins brown.

Abdomen.—Deep brown, somewhat brighter laterally on 1st and 2nd tergites, and with dark brown hairs. There are narrow, pale grey to yellowish, white-haired apical margins to the tergites, expanded into small median triangles, largest on 2nd and 3rd tergites, and also widening laterally, particularly on 1st tergite. Venter with the ground colour somewhat lighter, and the pale bands more uniform in width. Genitalia as in Figure 82, cerci rounded.

Male

Similar to ♀, but more hairy. Eyes with upper facets but little enlarged, and not clearly differentiated from the lower. There is a note by Ferguson on the allotype that the eyes in life were “blackish above, purplish beneath, and with one green-blue bar”. Parafacials and face more hairy than in ♀, and with quite dense long greyish hairs in the facial groove. Palpi similar in shape to those of *lunulata*

(Fig. 72), dark greyish brown, with brown hairs. Thorax with upper mesopleural convexity densely covered with long brown hairs. Deep brown of femora contrasting more strongly with the paler tibiae than in ♀. Apical edges of abdominal tergites bright brown, rather than greyish. Genitalia similar to those of *lunulata* (Figs. 15, 23), except that the ventral lobe on the style appears to be larger, and the cerci are rounded distally.

Distribution.—NEW SOUTH WALES: Leura, Jan.; Wentworth Falls, Dec.; Blackheath, Jan., Ferguson; Blue Mts., Jan., Ferguson.

The silvester Group

There are six recognizable species in the group, and there may be more, because it is difficult to know where intraspecific variability ends. They are also more evenly spread across northern Australia than the *distincta* group, and there is more overlapping between their territories (Fig. 8). Consequently, they are more difficult to define succinctly.

KEY TO SPECIES OF THE *silvester* GROUP OF THE SUBGENUS PSEUDOTABANUS

Females

1. A bright yellow species, with contrasting black antennal style, and olive-yellow scutum. North-western Australia *fulvissima*, sp. nov.
Duller, black, brown, or greyish species, sometimes with abdomen partly yellowish; antennal style not strongly contrasting 2
2. Antennal plate nearly always with strong tooth (Figs. 87, 88); frons usually parallel or converging 3
Antennal plate with blunt or rounded dorsal angle (Figs. 84–86); frons diverging 4
3. An unusually elongate, greyish brown species; basal abdominal tergites bright yellowish brown, with clearly defined median dark vitta; callus markedly narrower than frons. Northern Territory *alcocki* (Sum.)
A less elongate, darker, dull brown species; basal abdominal tergites dark brown, with, at most, a trace of a median darker vitta; callus (Fig. 88) full width of frons at base, with a wide, irregular, often wrinkled extension. Northern Territory, north Queensland *obscura*, sp. nov.
4. A relatively large (usually 9–11 mm), black and grey species, with blackish antennae, palpi, and legs; abdomen with sharply defined pale apical bands and median triangles on tergites (Plate 1, Fig. 7); frons wide (index about 2.5). Eastern Queensland, New South Wales, Central Australia *silvester* (Bergr.)
Usually smaller (7–9 mm), brown to fawn or greyish, sometimes partly yellowish species, with brown to yellowish antennae and palpi, and predominantly brown legs; pale bands on abdominal tergites narrow or diffuse 5
5. A relatively slender, variable, brown to greyish or yellowish brown species; frons relatively narrow (index 3); callus not greatly widened at base (Fig. 86). North-western Australia to Cape York *tryphera* (Tayl.)
More solidly built, greyish species, with basal abdominal tergites yellowish laterally; frons wide (index 2–2.5); callus usually markedly widened at base, more or less anchor-shaped (Fig. 84). Western Australia *eyreana*, sp. nov.*

* Dark specimens of *eyreana* may be distinguished from *silvester* by the paler appendages, light yellowish anterior wing veins, yellowish hue of basal abdominal tergites, and usually differently shaped callus.

MESOMYIA (PSEUDOTABANUS) FULVISSIMA, sp. nov.

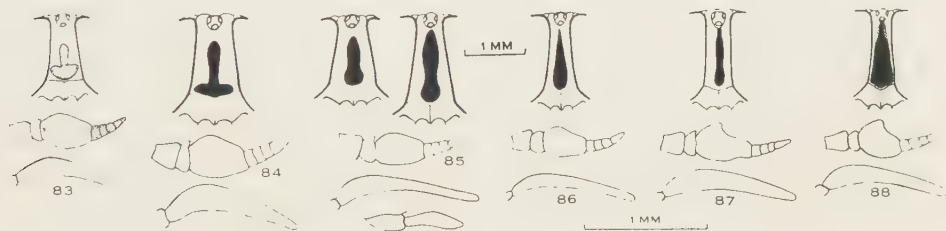
Type.—Holotype ♀, from Sir Graham Moore I., N.W.A., 20.ii.1945, B. Malkin, in the U.S. National Museum. Paratype ♀, with same data and agreeing with holotype, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—4 ♀♀.

A small, distinctive, bright yellow species; with strongly contrasting black antennal style; olive-yellow scutum; bright yellow legs, darkening on tarsi; brownish suffusion of wing in middle section anteriorly; bright yellow abdomen; and distinctive 8th sternite and gonopophyses (Fig. 95). Length 7–8 mm. It is possible that these specimens were originally preserved in alcohol, but, if so, they have dried out very well.

Female (Figs. 83, 95)

Head.—Frons moderately wide (index 2.5), diverging, with fawn-yellow tomentum, and short, inconspicuous, rather sparse brown hairs; ocellar tubercle greyish fawn, prominent; callus bright brownish yellow, transverse and almost full width of frons at base, and with a short, wide, tapering extension; the appearance, however, is not like that of the *lunulata* group. Subcallus light yellow, thinly



Figs. 83–88.—The *silvester* group of subgenus *Pseudotabanus*, ♀♀, except palp of ♂ in 85: 83, *fulvissima*, sp. nov.; 84, *eyreana*, sp. nov.; 85, *silvester* (Bergr.), showing variation in frons; 86, *tryphera* (Tayl.); 87, *alcocki* (Sum.); 88, *obscura*, sp. nov.

tomentose, without hairs; parafacials and face light yellow, parafacials with yellow hairs, face almost hairless. *Antennae*: 1st and 2nd segments creamy yellow, with brownish yellow hairs; basal plate of 3rd bright yellow, darkening distally; style black. Palpi yellow, with short creamy yellow hairs on 1st segment, inconspicuous brown ones on 2nd, and a distinct bare area, not seen in any other species of the group except *eyreana*, on the basal third of the 2nd segment. Beard sparse, creamy yellow.

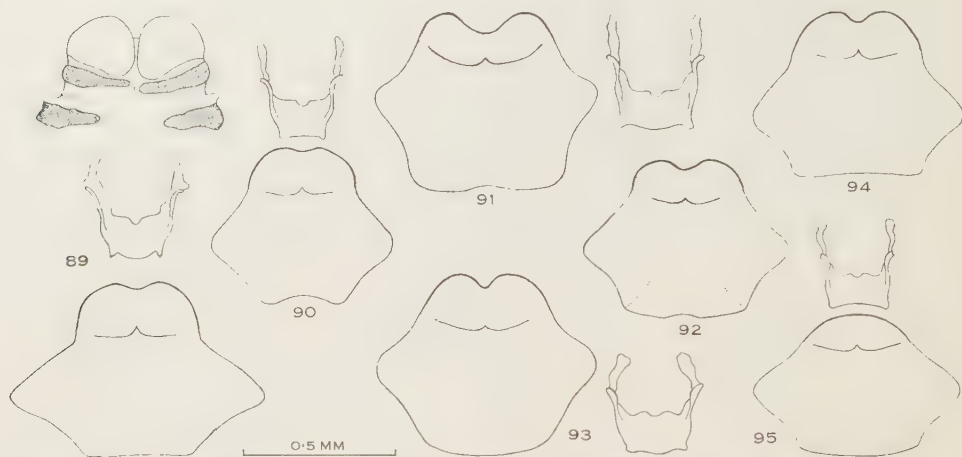
Thorax.—Scutum and scutellum with underlying ground colour brownish black, but hidden by dense greyish yellow tomentum; dorsocentral vittae and lateral areas yellow, fading behind suture; hairs obscure brown on disc, yellowish on lateral margins and around scutellum. Pleura light fawn-yellow, with light yellowish brown and cream hairs.

Legs.—Coxae brighter yellow than pleura, with yellowish cream hairs; femora and tibiae bright yellow, with creamy to brownish yellow hairs; tarsi darkening progressively to almost blackish brown on distal segments, with some yellowish hairs basally, but predominantly dark brown.

Wings.—Greyish, with costal cell brown, and a dark brown suffusion along R_s and R_{4+5} as far as fork, narrowly across base of discal cell, and along basal section of Cu_1 ; stigma dark brown, conspicuous; veins yellowish brown anteriorly and posteriorly, dark brown more distally; R_1 angulate, and with short appendix.

Abdomen.—Bright yellow, with apices of tergites paler, and ground colour vaguely darker on distal tergites. Hairs bright yellow, mixed with a few darker ones in sublateral areas. Venter similar to dorsum, but hairs paler.

Distribution.—NORTH-WESTERN AUSTRALIA: Sir Graham Moore I., Feb., Malkin.



Figs. 89–95.—The *silvester* group of subgenus *Pseudotabanus*, ♀ genitalia: 89, *silvester* (Bergr.); 90, *tryphera* (Tayl.); 91 and 92, *alcocki* (Sum.), usual form and variant; 93, *obscura*, sp. nov.; 94, *eyreana*, sp. nov.; 95, *fulvissima*, sp. nov.

MESOMYIA (PSEUDOTABANUS) ALCOCKI (Summers)

* *Silvius alcocki* Summers, 1912, p. 227; Ricardo 1915c, p. 259; Surcouf 1921, p. 142; Enderlein 1925, p. 314. Two cotype ♀♀, from Darwin, N.T., S. L. Strangman, formerly in the London School of Hygiene and Tropical Medicine, now in the British Museum (Natural History). Not Taylor 1916, pp. 806, 815; Ferguson 1921a, p. 368 (both = *obscura*, sp. nov.).

Mesomyia (Pseudotabanus) alcocki (Summers). Mackerras 1955b, p. 607.

Silvius marginatus Taylor, 1916, p. 806; Ferguson 1921a, p. 369; nec Walker, 1848.

The species have been misidentified in Australian collections, this one being mistaken for *marginatus* Walker (= *tryphera* Taylor) and *obscura*, sp. nov. being identified as *alcocki* Summers.

Material examined.—38 ♀♀.

A slender brown species; with callus markedly narrower than frons at base; dark brown, strongly toothed antennal plate; vittate scutum; faintly brownish wings; and abdomen with yellowish brown basal tergites, and well-defined pale apical bands and median black vitta. Length 8–10 mm.

Female (Figs. 87, 91, 92; Plate 1, Fig. 8)

Head.—Frons usually parallel to slightly converging, occasionally slightly diverging, index 3–4, with fawn-grey tomentum and short inconspicuous dark hairs;

callus dark brown, oval at base, with more or less of a narrowed waist leading into a broad extension to the anterior ocellus. Subcallus, parafacials, and face greyish cream, with fine white hairs, only a few on subcallus lateral to antennae. *Antennae*: 1st and 2nd segments yellowish brown, with some greyish overlay and short black hairs; 3rd dark brown, paler at base, with strong dorsal tooth and blackish brown style. Palpi yellowish cream, 2nd segment with short black hairs. Beard sparse, white.

Thorax.—Scutum with dark ground colour reduced to 3 stripes by the wide, rather diffuse, greyish dorsocentral vittae and lateral areas; a narrow dark brown median line anterior to suture. Hairs on disc short, mainly dull yellowish cream, mixed dull yellowish cream and brown on notopleural lobes, and paler on scutellum; supra- and postalar tufts barely differentiated. Pleura grey, with dull cream hairs.

Legs.—Coxae like pleura; other segments dark to blackish brown, with yellowish knees, and dark brown hairs, except for white ones on mid and hind femora.

Wings.—Greyish, with a faint brown tint; stigma dark brown, conspicuous; veins brown; R_4 without appendix.

Abdomen.—A variable number of basal tergites light yellowish brown, darkening progressively posteriorly, the apical tergites being dark brown: 1st to 4th with prominent fawn-cream apical bands, which widen laterally, 5th and 6th with narrow apical bands, 7th entirely dark; an interrupted median black vitta on 3 or 4 basal tergites, merging into the dark colour posteriorly. Hairs black on discs, creamy white on apical and lateral margins of tergites. Venter with first 3 sternites pale fawn-brown, apical sternites darkening progressively, all with cream apical margins; hairs white on the paler areas, mainly black on more distal sternites.

The description is based on fresh specimens. Older ones are lighter in general colour, with the antennal plate and legs brighter brown. Two rather small ♀♀ from Berry Springs have the 8th sternite (Fig. 92) more like that of *obscura*, but pale and lightly chitinated; they agree in external characters with normal specimens from the same locality.

Distribution.—NORTHERN TERRITORY: Berrimah, biting, Nov., I.M.M.; Darwin, Nov. Hill, Hunt; Howard Springs, Dec., O'Gower; Berry Springs, Nov., O'Gower; Humpty Doo, Oct., Crawford; Mataranka.

MESOMYIA (PSEUDOTABANUS) OBSCURA, sp. nov.

Silvius alcocki Taylor, 1916, pp. 806, 815; Ferguson 1921a, p. 368; nec Summers, 1912 (see explanation under *alcocki*).

Type.—Holotype ♀, from 34 miles S. of Darwin, N.T., G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—19 ♀♀.

A small, slender, brown species; with brown antennae, palpi, and legs; a faint brownish tint in the wings; and a uniformly brown abdomen, with narrow pale bands on tergites, and, at most, a trace of a darker median vitta. Length 7.5–9 mm. To be distinguished from *alcocki* by darker colour, wider, differently

shaped callus, absence of a dark median vitta on abdomen, and differently shaped 8th sternite; and from *tryphera* by the usually parallel or converging frons, differently shaped callus, and darker, differently shaped antennal plate.

Female (Figs. 88, 93)

Head.—Frons parallel or converging, occasionally slightly diverging, index 3–4, with brownish fawn tomentum, except for a narrow pale line at eye margins, and inconspicuous dark hairs; callus dark brown, bulging and full width of frons below, black, flat, and wrinkled above, tapering into a flat band to anterior ocellus. Subcallus, parafacials, and face with pale grey to light fawn tomentum and brown hairs. *Antennae*: 1st and 2nd segments yellowish brown, with some grey tomentum and black hairs; 3rd dark brown, basal plate wide, and nearly always with a strong tooth, or at least a sharp dorsal angle. Palpi brown, with brown hairs. Beard sparse, dull cream.

Thorax.—Scutum and scutellum dark dull brown, with the dorsocentral vittae and lateral areas somewhat greyish, and the sublateral brown colour a little darker than the rest; hairs dark brown to black. Pleura brownish grey, with bright to dull brown hairs.

Legs.—Coxae similar to pleura; remaining segments dark brown, with dark brown to black hairs.

Wings.—Greyish, with a brown tint, especially anteriorly; stigma dark brown; veins brown; R_4 without appendix.

Abdomen.—First tergite greyish brown, dark in centre, and with slightly paler apical margin; remaining tergites progressively darker brown, 5th to 7th almost black, all with rather narrow grey apical margins, which may widen somewhat laterally; hairs dark brown to black, sometimes with some white ones at apical lateral corners of tergites. Venter dark greyish brown, with pale grey apices to the sternites; hairs dark brown, except for a few pale ones in apical fringes.

The Queensland specimens are not quite as dark as those from the Northern Territory, have wider pale bands on the abdominal tergites, and the frons is parallel to slightly diverging. The genitalia are similar in the two forms, which may represent incipient subspecies.

Distribution.—NORTHERN TERRITORY: near Darwin, Jan., Hill; 34 miles S. of Darwin, Hill; Daly R., Jan., Crawford. QUEENSLAND: Stewart R., Jan., Feb., Hale and Tindale; Bathurst Head, Jan., Hale and Tindale.

MESOMYIA (PSEUDOTABANUS) TRYPHERA (Taylor)

* *Tabanus marginatus* Walker, 1848, p. 189. Type ♀, from N. or N.W. Australia, in the British Museum (Natural History). Not *Tabanus marginatus* Macquart, 1848, Neotropical; homonymy noted by Fairchild 1956, p. 22.

Silvius marginatus (Walker). Ricardo 1901, p. 296, 1915a, p. 279, 1915c, p. 259; Froggatt 1911, p. 13; Surcouf 1921, p. 143. Not Taylor 1916, p. 806; Ferguson 1921a, p. 369 (both = *alcocki* Summers). Not *Silvius marginatus* Macquart, 1838 (= *Pseudacanthocera sylvierii* (Macquart, 1838), Neotropical); homonymy noted by Fairchild 1956, p. 23.

Mesomyia (Pseudotabanus) marginata (Walker). Mackerras 1955b, p. 607.

* *Silvius trypherus* Taylor, 1916, p. 811; Ferguson and Hill 1922, p. 250. Type ♀, from Boorooloola, N.T., 23.i.1912, M. S. Giles, in the School of Public Health and Tropical Medicine, University of Sydney. This form agrees with the type of *marginatus* Walker.

* *Silvius elongatulus* Taylor, 1916, p. 812; Ferguson and Hill 1922, p. 250 (syn. of *trypherus* Taylor). Type ♀, from Stapleton, N.T., 2.i.1913, G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

* *Silvius elongatulus* var. *persimilis* Taylor, 1919, p. 43; Ferguson and Hill 1922, p. 250 (syn. of *trypherus* Taylor). Type ♀, from Brock's Creek, N.T., G. F. Hill, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—125 ♀♀.

A small, slender, fawn-brown to greyish or yellowish brown species; basal plate of antenna with obtuse or rounded dorsal angle; pale bands on abdominal tergites usually diffusing into the darker colour, and not very conspicuous. Length 7.5–9 mm.

Female (Figs. 86, 90)

Head.—Frons diverging, index 3, with pale creamy fawn tomentum and short creamy white hairs; callus dark brown, slightly more than one-third width of frons at base, and tapering evenly to below anterior ocellus. Subcallus, parafacials, and face greyish cream, with inconspicuous short creamy white hairs. *Antennae*: 1st and 2nd segments light brown, 1st with some ashy tomentum, both with short black hairs; 3rd with basal plate orange brown, darkening apically to the brown style. Palpi fawn-brown to yellowish brown, with short brown hairs. Beard sparse, dull cream.

Thorax.—Scutum and scutellum rather evenly brownish fawn, the sublateral ground colour sometimes a little darker; median and dorsocentral vittae at most vaguely indicated; hairs short, creamy gold, with a few darker ones in front of wing root. Pleura light grey, with greyish white hairs.

Legs.—Coxae similar to pleura; remaining segments brown, with mainly brown hairs, but dull cream ones on mid and hind femora.

Wings.—Slightly greyish; stigma and veins light brown, more yellowish at base; R_4 without appendix.

Abdomen.—Variable; tergites in some specimens dull fawn-brown, fading to paler greyish fawn at apical margins; in others yellowish brown, with creamy yellow apical margins, and, occasionally, incipient paler median triangles; hairs brown on the darker parts, dull creamy yellow on the paler apical and lateral margins. Venter similar to dorsum, and showing the same kind of variation, but with a generally more greyish appearance; hairs short, cream.

The dark form with the fawn-brown tomentum is *tryphera* (= *marginatus*). The paler form with more greyish scutum, yellowish abdomen, and indication of median pale triangles on tergites is *persimilis*, and appears to be the commonest; *elongatulus* is intermediate; both have yellowish antennal plates, which are sometimes unusually wide and rounded dorsally. Specimens from north-western Australia are particularly dark. One of them has an unusually wide frons, and

some of the others have a vittate scutum like *silvester*. They are not in very good condition, and more material will be needed to settle their identity.

Distribution.—NORTH-WESTERN AUSTRALIA: Sir Graham Moore I., Feb., Malkin; Port George IV, Feb., Paull; Wyndham, Feb., Lukins; Port Hedland, Feb., Marlow. NORTHERN TERRITORY: Darwin, Hill, McEachern; Batchelor, Dec., Hill; Stapleton, Jan., Hill; Adelaide R., Dec., Woodhill; Brock's Ck., Dec., Jan., Feb., Campbell, Hill; Daly R., Jan., Crawford; Adelaide R. to Larrimah, Dec., Woodhill; Larrimah, Dec., Woodhill; Mataranka; Groote Eyelandt, Tindale; Boorooloola, Jan., Giles. QUEENSLAND: Mapoon, Dec.

MESOMYIA (PSEUDOTABANUS) SILVESTER (Bergroth)

* *Silvius silvester* Bergroth, 1894, p. 71; Ricardo 1901, p. 296, 1915c, p. 259; Froggatt 1911, p. 13; Taylor 1916, p. 806; Surcouf 1921, p. 143. The type ♀, from "Coomooboolaroo", near Duaringa, C. Qld., H. G. Barnard, in the Frey Collection, University Zoological Museum, Helsingfors, was kindly sent to me by Dr. W. Hackman, and proved to be identical with the species commonly known as *australis* Ricardo.

* *Silvius australis* Ricardo, 1915c, p. 263; Taylor 1916, p. 806, 1917a, p. 753, 1918, p. 62; Ferguson 1916, p. 205, 1920, p. 132, 1921a, p. 368; Surcouf 1921, p. 142; Enderlein 1925, p. 314. Type ♀, from Stannary Hills, N. Qld., T. L. Bancroft, in the British Museum (Natural History).

Mesomyia (Pseudotabanus) australis (Ricardo). Mackerras 1955b, p. 607, fig. 14.

Material examined.—1 ♂, 194 ♀ ♀.

A small, slender, blackish species; with wide, diverging frons; dark to blackish brown antennae, palpi, and legs; well-defined scutal vittae; clear wings; and conspicuous greyish white apical bands and median triangles on abdominal tergites. Length 7.5–11 mm.

Female (Figs. 85, 89; Plate 1, Fig. 7)

Head.—Frons wide, diverging, index about 2.5, with ashy grey tomentum and inconspicuous whitish hairs; ocellar tubercle grey to brownish; callus black, about one-third width of frons at base, more or less rounded below, typically with a waist about junction of its lower and middle third, above which it is expanded somewhat, and then tapers gently to ocelli. Subcallus, parafacials, and face with ashy grey tomentum and short inconspicuous white hairs. *Antennae*: 1st and 2nd segments blackish brown, with pale grey tomentum on 1st, and black hairs; 3rd deep to blackish brown. Palpi dark to medium brown, with some whitish hairs on 1st segment, and inconspicuous black ones on 2nd. Beard scanty, white.

Thorax.—Ground colour of scutum dark brown, but so reduced by the wide grey dorsocentral vittae and lateral areas that the appearance is of a greyish scutum with 3 broad brown stripes; hairs short, mixed brown, dull creamy yellow, and creamy white. Scutellum brown at base, grey apically, with dull creamy yellow and creamy white hairs. Pleura pale grey, with greyish white hairs.

Legs.—Coxae like pleura; remaining segments deep brown to brownish black; mid and hind femora with dark brown and greyish white hairs; remaining segments with dark brown and blackish hairs.

Wings.—Faintly grey; stigma dark brown; veins brown, paler at base; R_4 sometimes with a rudimentary appendix.

Abdomen.—Tergites deep to blackish brown, with dark brown hairs; apical margins grey, with greyish white hairs. The pale colour is expanded in the mid-line on 2nd tergite to form a well-defined median triangle, which sometimes extends so far as to divide the brown completely into two parts; there are also variable median expansions on other tergites, especially 3rd and 4th, and pale lateral expansions which are particularly well marked on 1st to 3rd. Venter with 1st and 2nd sternites almost entirely light grey; remainder brown, with apical grey bands; all with greyish white hairs.

Male (Figs. 16, 24, 85)

I have seen a single ♂ from Townsville, identified by G. F. Hill as *Silvius australis*. Eyes large, contiguous; upper facets markedly enlarged, bright brown, and clearly marked off from the smaller, blackish, lower and posterior facets. Subcallus, parafacials, and face pale cream, with white hairs. *Antennae*: 1st and 2nd segments light brown, with some ashy tomentum and black hairs; 3rd bright brown ventrally at base, remainder dark brown, the basal plate narrower than in ♀, and showing distinct indications of subdivision. Palpi greyish fawn, with long dark brown and a few whitish hairs. Dorsocentral vittae on scutum barely perceptible, and lateral areas with a fawn tint. Pleural hairs more yellowish cream.

First 4 tergites of abdomen bright yellowish brown, with pale creamy brown apical margins, which appear somewhat ashy in certain lights; subsequent tergites deep brown, with brownish grey apical margins, much as in ♀. Venter with first 3 sternites creamy yellow, paler apically; remainder dark brownish grey, with narrow pale apical margins; all with yellowish cream hairs.

Distribution.—QUEENSLAND: Gilbert R., Mar., Kenny; Cape York (Bamaga, Skull Ck.), May, M.J.M.; Claudie R., Feb., Kershaw; Mt. Tozer, Dec., Wassell; Lockhart R., Flint; Flinders I., Jan., Hale and Tindale; Double I., Jan., McCulloch; Kuranda, Jan., Dodd, Roberts; Cairns, Illingworth, Taylor; Gordonvale, Feb., Hitchcock; Mutchilba, Feb., Selby; Stannary Hills, Bancroft; Palm I., Dec., Jan., M. & M., Taylor; Magnetic I., Feb., Hill, Taylor; Townsville, Jan., Feb., Mar., Fielding, Hill, O'Gower, Taylor; Ching Do, Taylor; Bowen (Port Denison); Rockhampton: Duaringa, Barnard; Gladstone, Nov., Dec., Poggioli; Eidsvold, Oct.–Apr., Bancroft; Kilcoy, Dec., Norris; Brisbane, Mar., Byrne, Denmead; Mt. Crosbie, Jan., Derrick; Camp Cable, Nov., I.M.M.; National Park (low level), Dec. NEW SOUTH WALES: Brewarrina, Dec., Quinn; Cobar, Jan. CENTRAL AUSTRALIA*: Arltunga, Feb., Noblet.

MESOMYIA (PSEUDOTABANUS) EYREANA, sp. nov.

Type.—Holotype ♀, from Mundiwindi, W.A., without other data, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—13 ♀♀.

A rather thickset species; resembling *silvester*, but distinguished by differently shaped callus, and yellow to yellowish brown antennal plate, palpi, anterior wing veins, and sides of first 2 or 3 abdominal tergites. Length 7.5–9 mm.

Female (Figs. 84, 94)

Head.—Frons wide, diverging, index 2–2.5, with fawn-grey tomentum and inconspicuous dark hairs; callus dark brown, transverse and about three-fourths

* This term seems more appropriate than Northern Territory here, as the locality is far removed from the more northerly records.

width of frons at base, with an irregular median extension ending below anterior ocellus—the appearance is often anchor-like. Subcallus, parafacials, and face light grey, with white hairs, those on subcallus limited to area lateral to antennae. *Antennae*: 1st and 2nd segments light yellowish brown, 1st with grey tomentum, both with short black hairs; 3rd with basal plate bright to yellowish brown, sometimes darkening distally; style deep to blackish brown, not as contrasting as in *fulvissima*. Palpi fawn-brown; 2nd segment with a yellowish bare area on basal third above, and short black hairs. Beard sparse, greyish white.

Thorax.—Scutum as in *silvester*, but vittae narrower, and a yellowish hue on shoulders and lateral areas. Pleura grey, with dull cream hairs.

Legs.—Coxae as pleura; other segments deep to blackish brown, except for a variable yellowish suffusion on basal fourth or more of tibiae in some specimens. Hairs predominantly black.

Wings.—Faintly greyish; stigma reduced, inconspicuous; veins bright yellowish on basal two-thirds anteriorly, brown distally and posteriorly, the yellow colour of *R* and *R*₁ usually conspicuous; *R*₄ strongly curved, sometimes angulate, without appendix.

Abdomen.—Dark brown, variably yellowish laterally on first 3 tergites; with dull fawn apical bands, narrowing posteriorly, on all tergites, and indications of median triangles on 2nd to 4th, more basally situated than in *silvester*; hairs predominantly dull cream (specimens rubbed). Venter light yellowish brown basally, darkening on apical sternites, with paler apical bands, and predominantly white hairs anteriorly, black ones posteriorly.

The ♀♀ from Port Hedland are not in good condition, but they appear to be paler, and to have a somewhat narrower callus. The gonopophyses also seem to be slightly different, but the material is not good enough to distinguish these specimens from those from further south.

Distribution.—WESTERN AUSTRALIA: "Woodstock," Port Hedland, Feb., Marlow; Mundiwindi; Sandstone, Apr., Michel.

Subgenus MESOMYIA Macquart

For taxonomic details see p. 849.

Female

Medium-sized to small, usually hairy, often *Dasybasis*-like species. Eyes perceptibly hairy at $\times 15$; unbanded. Frons wide to medium (index 2 to 3.5), usually diverging, occasionally parallel; callus linear, club-shaped, or short and wide with median extension. Subcallus and face tomentose. First antennal segment occasionally swollen, but not hood-like dorsally; 3rd with 4-annulate style. Palpi variable, even within species, from *distincta*-like to short, plump, and soft, occasionally spatulate, rarely with depressed bare area. Proboscis usually strong, sometimes quite short and soft. Wing with vein *sc* bare or setulose below. Genitalia larger, relative to the size of the insects, than in other Australian subgenera, but otherwise undistinguished.

Male

Eyes as hairy as in ♀♀; upper facets slightly to considerably enlarged. Palpi variable, but usually wider, more conical, and more pointed at tip than in other subgenera; without detectable apical pit. Style of hypopygium without ventral lobe.

Two striking features of the Australian species are the inconstancy of setulae on *sc*, and a greater degree of variation in the male genitalia than has been seen elsewhere in the tribe. Three archaic species — *cydister*, *tepperi*, *latifrons* — have *sc* bare, like the African species, which suggests that setulae were acquired by the ancestors of the other species of *Mesomyia* and the groups of *Pseudotabanus* after the tribe became established in Australia. The genitalia show three types of styles. Those of *cydister* (Fig. 29) are remarkably like the styles of the almost equally primitive African *M. (Perisilvius) monticola* (Neave), and may approximate to the ancestral form. *M. (M.) imitator* (Fig. 30) has retained styles of this type, and so has *M. (Ps.) silvester* (Fig. 24). On the other hand, the presumed male of *latifrons* (Fig. 28) has styles which are like the form seen in the *distincta* group (Fig. 22), but lacking the ventral lobe; while the *montana* complex (Figs. 25–27) shows a trend towards truncation of the styles, paralleling changes that occurred in the evolution of the Tabaninae. None of these species, except possibly *cydister*, can be regarded as a surviving ancestral relict, but they do illustrate the ways in which important evolutionary developments have occurred.

Most of the species are easy to place subgenerically by the obviously hairy eyes in both sexes. On the east coast, however, there is a progressive decrease from south to north in size of body, general hairiness, and length and density of hairs on the eyes, culminating in the northern *doddi*, which is a small, smooth species, with ocular hairs that can often be seen only at appropriate angles of illumination. This gradation with latitude, considerable variation within local populations, and a tendency for old specimens to fade, have made it difficult to assess the eastern forms, and the genitalia have given no assistance in resolving the problem. The known Western and South Australian species, on the other hand, are sharply distinguished, and should present no difficulty.

KEY TO AUSTRALIAN SPECIES OF THE SUBGENUS MESOMYIA

Females

1. Callus linear (Figs. 96–98); frons medium (index 2.5–3.5)2
 Callus club-shaped or wide; frons usually wider4
2. Basal plate of 3rd antennal segment wide, with strong tooth which is often distinctly hooked; a robust species (11–13 mm). Western Australia*sulcifrons* (Ferg.)
 Basal plate of 3rd antennal segment narrower, tooth, if developed, relatively weak.
 Eastern Australia3
3. A small (8–10 mm), slim, smooth, yellowish brown species, with the yellowish apical bands on abdominal tergites inconspicuous. North Queensland*doddi* (Ric.)
 A larger (usually 10–14 mm*), stouter, more hairy, usually much darker species, with better defined, usually cream to white apical bands and median triangles on abdominal tergites. Southern New South Wales to north Queensland*montana* (Ric.)

* One dark, northern ♀ 7 mm.

4. Callus club-shaped, much narrower than frons (Figs. 100, 101). South Australia5
 Callus short and wide, with median extension (Figs. 99, 102, 103). Western Australia6
5. A medium-sided (14 mm), dark brown species, with relatively narrow frons (index 3)*tepperi* (Ferg.)
 A large (17 mm), dark grey species, with wide frons (index 2)*latifrons*, sp. nov.
6. Basal plate of 3rd antennal segment slender, with gently curved dorsal surface (Fig. 109);
 a relatively long-bodied (12–14 mm), hairy species, with relatively wide apical pale
 bands and small median triangles on abdominal tergites*cydister* (Tayl.)
 Basal plate of 3rd antennal segment wide, with more definite dorsal angle (Figs. 110,
 111); smaller (10–11 mm), broader, less hairy species7
7. A lighter-coloured species, with broader frons (index 2), clearly defined scutal vittae, and
 conspicuous pale median triangles on abdominal tergites*imitator* (Ferg.)
 A very dark species, with narrower frons (index 2.5–3), obscure scutal vittae, and
 no pale median triangles on abdominal tergites*nigerrima*, sp. nov.

MESOMYIA (MESOMYIA) DODDI (Ricardo)

* *Silvius doddi* Ricardo, 1915c, p. 261; Taylor 1917a, p. 752, 1918, p. 63; Surcouf 1921, p. 142; Enderlein 1925, p. 314. Type ♀, from Kuranda, N. Qld., F. P. Dodd, ♂, from Herberton, N. Qld., F. P. Dodd, in the British Museum (Natural History).

Mesomyia (*Mesomyia*) *doddi* (Ricardo). Mackerras 1955b, p. 609.

Material examined.—3 ♂♂, 30 ♀♀.

A small, slender, yellowish brown species; with linear callus; faintly brownish wings, which are slightly darker anteriorly; and more or less definite yellowish apical bands on abdominal tergites. Length 8–10 mm.

Female (Figs. 97, 105, 119)

Head.—Eyes with short, sometimes inconspicuous, pale hairs. Frons diverging, index 3.5, with yellowish fawn tomentum, somewhat darkened towards the middle, and fairly dense brown hairs; callus brown, full length of frons, sometimes expanded a little at lower end. Subcallus, parafacials, and face fawn-brown, with brown hairs, which are unusually prominent on the subcallus. *Antennae*: 1st and 2nd segments yellowish cream, with brown hairs; 3rd brownish yellow, sometimes darkening on style, plate with some short black hairs behind the rounded dorsal angle. Palpi fawn; 1st segment with brown hairs; 2nd with fairly dense short blackish hairs. Beard dull yellowish cream, rather sparse.

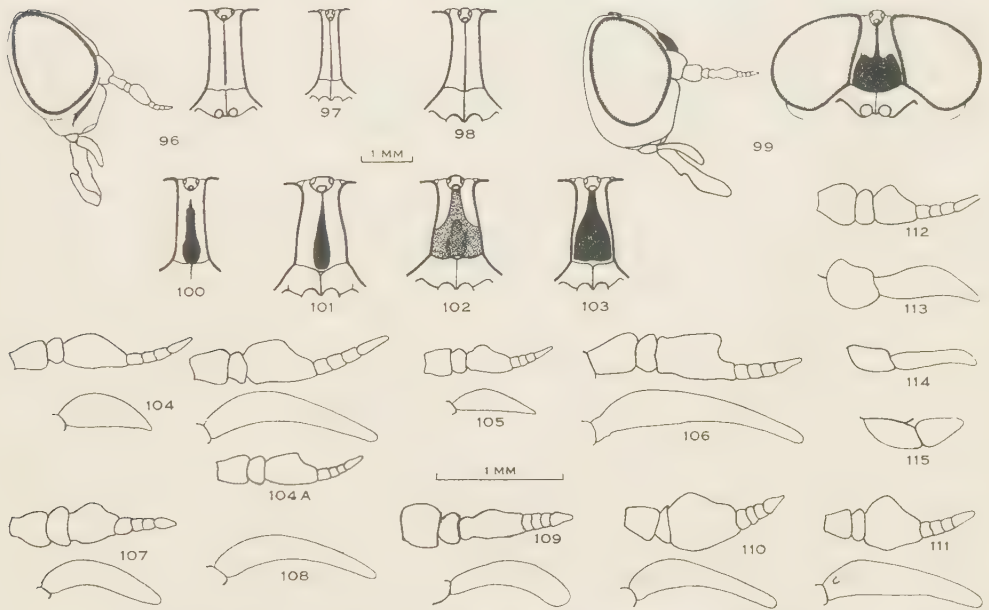
Thorax.—Scutum light brown, with a yellowish tint on either side of the median line, dorsocentral vittae inconspicuous, and a greyish hue in the lateral areas; hairs short, yellowish, with brown ones anteriorly and laterally. Scutellum a little paler than scutum, with yellowish brown hairs on disc and light brown ones apically. Pleura light greyish fawn, with dull cream to light brown hairs.

Legs.—Coxae similar to pleura. Femora light yellowish brown, fore and mid with brown and dull yellowish hairs, hind mainly with yellowish hairs. Tibiae

and tarsi a little darker, especially on hind legs; hairs brown, becoming black on tarsi.

Wings.—Light greyish brown, darker in the costal cell; stigma brown; veins light brown; *sc* setulose below; R_4 without appendix.

Abdomen.—Light brown, with yellowish hue on basal 3 tergites, more uniformly brown on apical tergites; all with paler apical bands, which are yellowish on the first 3, greyish, less conspicuous on the others; sometimes indications of paler median apical triangles on 2nd and 3rd; hairs light brown to dull golden. Venter paler than dorsum, and with apical banding of sternites less evident; hairs bright golden.



Figs. 96-115.—Subgenus *Mesomyia*, ♀♀, except last four: 96 and 104, *montana* (Ric.), showing range of variation in antennae and palpi (left, *montana* form from Mt. Tamborine, S.Qld.; right, *niger* form from Tinderry, N.S.W.; 104A, slender form from Stradbroke I., S.Qld.); 97 and 105, *doddi* (Ric.); 98 and 106, *sulcifrons* (Ferg.); 99 and 109, *cydister* (Tayl.); 100 and 107, *tepperi* (Ferg.); 101 and 108, *latifrons*, sp. nov.; 102 and 110, *imitator* (Ferg.); 103 and 111, *nigerrima*, sp. nov.; 112, antenna of presumed ♂ of *latifrons*; 113-115, palpi of ♂♂ of: 113, *montana*; 114, *imitator*; 115, *cydister*.

Male (Fig. 25)

Similar to ♀, but somewhat darker. Eyes densely hairy; upper facets but little enlarged, and not differentiated from lower. Subcallus, parafacials, and face with quite long brown hairs. Palpi similar in shape to those of ♀, but with longer and denser dark brown hairs.

Distribution.—QUEENSLAND: Kuranda, Dodd, Taylor; Freshwater Ck., near Cairns, Sept., M. & M.; Cairns, Dodd; Meringa, Sept., Burns; Bramston Beach, Sept., M. & M.; Herberton.

MESOMYIA (MESOMYIA) MONTANA (Ricardo)

* *Silvius montanus* Ricardo, 1917, p. 216; Surcouf 1921, p. 143; Ferguson 1921*a*, p. 371, 1926*a*, p. 301; Ferguson and Hill 1922, p. 246 (possibly *Mesomyia*). Type ♀, from Mt. Tamborine, S. Qld., A. M. Lea, in the South Australian Museum, Adelaide.

Mesomyia (Mesomyia) montana (Ricardo). Mackerras 1955*b*, p. 609, figs. 15 *A, H*.

* *Silvius niger* Ricardo, 1917, p. 215; Taylor 1919, p. 45; Surcouf 1921, p. 143; Ferguson 1926*a*, p. 301. Type ♀, from Helensburgh, N.S.W., March, E. W. Ferguson, in the British Museum (Natural History). Individual specimens appear very different, as are the types, but black *niger* merges in all characters into brown *montana*, which I have given precedence as it is the better-known name.

Mesomyia niger (Ricardo). Surcouf 1921, p. 144 (he listed the species twice, in different genera); Ferguson and Hill 1922, p. 246 (generic assignment doubtful); Mackerras 1955*b*, p. 609, figs. 15 *C, D, J, L*.

Veprius niger (Ricardo). Enderlein 1925, p. 315.

* *Silvius angusticallosus* Taylor, 1919, p. 44; Ferguson 1926*a*, p. 301. Type ♀, from Stradbroke I., S. Qld., 3.xii.1912, H. Hacker, in the Queensland Museum, Brisbane. The type agrees with the brown *montana* form of the species.

Material examined.—10 ♂♂, 88 ♀♀.

A medium-sized, usually moderately stout, very variable, usually dark brown to blackish species, with a linear callus. Length 10–14 mm (one northern ♀ 7 mm). The southern, darker form will be described first.

Female (Figs. 96, 104, 116–118)

Head.—Eyes with dense brown hairs. Frons diverging, index 2.5–3, with mainly brown tomentum and strong dark brown hairs; callus blackish brown, linear, full length of frons. Subcallus, parafacials, and face brown, with some greyish reflections; subcallus with a group of strong black hairs lateral to antennae; parafacials with long black and creamy white hairs; face with shorter hairs, which are mainly black. *Antennae*: 1st segment with dark fawn tomentum and strong black hairs; 2nd dark brown, with black hairs; 3rd with basal plate variable in colour and shape, from reddish brown to blackish, often paler at base, and from rounded above to distinctly toothed; style dark brown to black. Palpi fawn-brown, 2nd segment with quite strong black hairs. Beard brown.

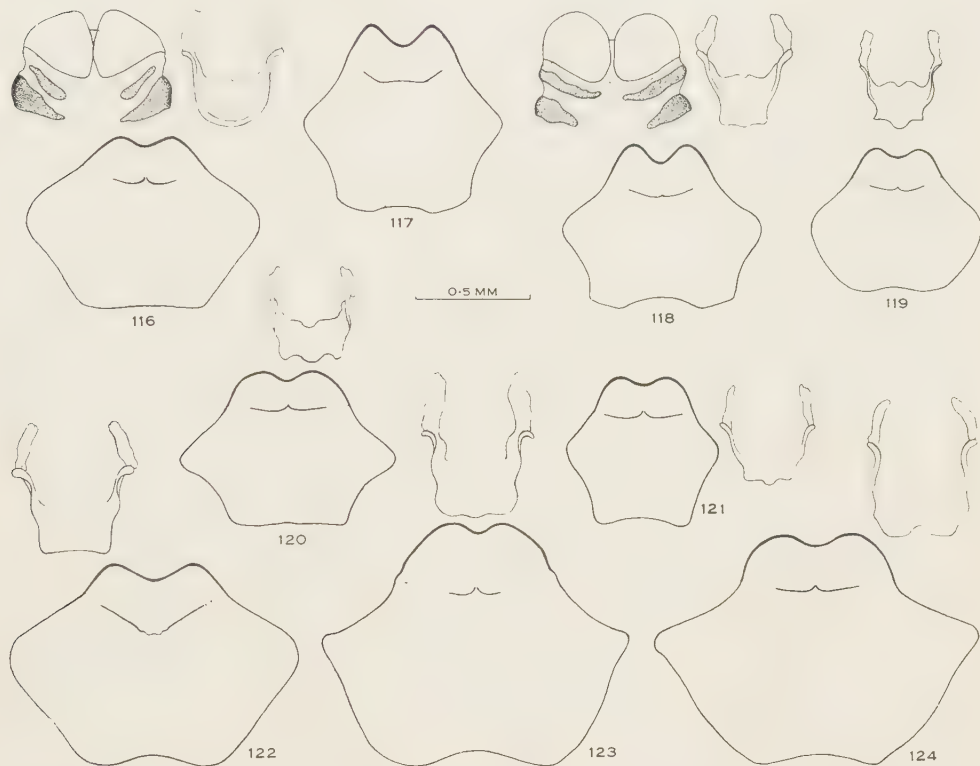
Thorax.—Scutum brownish black, with fairly evident greyish dorsocentral vittae, which fade behind the suture, and greyish lateral margins; hairs mixed black and light brown, stronger on lateral margins, where they are mainly black on notopleural lobes, and mixed dull yellowish cream and black above and behind wing root. Scutellum greyish black, with black hairs, except at extreme base. Pleura dark grey, with dull cream hairs, except for dark ones on upper mesopleural convexity.

Legs.—Deep brown to black, knees and tibiae variably paler; hairs black.

Wings.—Light brownish grey, with costal cell and stigma only slightly darker, sometimes with vague darkening more posteriorly; veins brown to dark brown; *sc* setulose below; *R*₄ usually without appendix.

Abdomen.—Black to brownish black, sometimes reddish at sides of 1st and 2nd tergites; 1st to 4th with paler apical margins, which are made conspicuous by

well-defined median triangles and sublateral zones of white hairs, contrasting with the deep brown hairs on the remainder of the tergites, and interrupted by the dark hairs reaching the apical edges on each side of the triangles; 5th and subsequent tergites entirely dark-haired. Venter brownish to greyish black, with black hairs, and paler, white-haired apical margins on 2nd to 4th sternites.



Figs. 116–124.—Subgenus *Mesomyia*, ♀ genitalia: 116–118, *montana* (Ric.), showing variation in 8th sternite, furca, and cerci (116 from Binna Burra, 117 pale form from Woodford, 118 from Beatrice R., all Qld.); 119, *doddi* (Ric.); 120, *imitator* (Ferg.); 121, *nigerrima*, sp. nov.; 122, *sulcifrons* (Ferg.); 123, *latifrons*, sp. nov.; 124, *cydister* (Tayl.).

Male (Figs. 26, 113)

More hairy than ♀. Eyes with long dense hairs, paler below; upper facets only slightly enlarged, and not sharply separated from lower. Hairs on basal segments of antennae, subcallus, parafacials, and face long, conspicuous. Palpi fusiform, tapering to a point, light fawn-brown, with long white hairs on 1st segment and dark brown ones on 2nd; inner surface of 2nd segment paler, bare. Scutal vittae ill-defined. Abdomen often more or less extensively light to yellowish brown at sides of 1st to 2nd or 3rd tergites and sternites; median triangles on 2nd to 4th tergites conspicuous, and dense long white hairs in lateral zones of same tergites; 5th to 7th entirely dark-haired. Venter with similar contrast between white-haired basal sternites and entirely dark-haired 5th to 7th.

Four intergrading forms of the species can be recognized. The first and second could be regarded as subspecies, and the fourth may be a sibling species, but more material would be necessary to settle their status.

The *niger* form extends from southern New South Wales into southern Queensland, where it merges into the *montana* form. It includes black and greyish white insects with white abdominal hair-tufts, and a moderately developed tooth on the basal plate of the antenna (right-hand specimen in Fig. 104) is relatively common. The eight known ♂♂ vary considerably, specimens from the Australian Capital Territory differing from those from Sydney and Barrington Tops described above in having the abdominal ground colour almost entirely dark and no dense lateral zone of white hairs. Southern ♀♀ also tend to be larger and more brightly patterned than northern ones, and it is possible that subspeciation may be developing between the populations in New South Wales.

The *montana* form is found mainly in the higher country of southern Queensland, but it also extends to the coast and far to the north. Only ♀♀ are known. They are typically brown, though often quite dark; hairs on eyes shorter than in the *niger* form; antennal plate usually rounded above, yellowish brown, contrasting moderately with the darker style; palpi extremely variable, from short and plump to quite long and slender; femora brown, tibiae more extensively yellowish; wings usually with more evident darkening across basal cells and along some of the veins; pale bands and triangles on abdominal tergites cream to light brown, with yellowish cream hairs. Two northern females from Beatrice R. differ only in having the paler abdominal hairs rich golden. The 7-mm specimen from Mt. Spec seems to belong here, but it could be a melanic form of *doddi*.

Two ♂♂ and 8 ♀♀ from coastal Queensland (Eungella to Woodford) are much paler than normal specimens, but I suspect that their distinctive appearance may be due to fading with age and exposure to light. The ♀♀ are light brown. Frons, parafacials, and face light greyish fawn, subcallus more brownish; basal antennal segments and palpi pale greyish fawn; antennal plate brownish yellow, style scarcely darkened; wings light brownish grey, with trace of darkening in costal cell only; pale bands on abdominal tergites cream, median triangles more yellowish, hairs creamy white. The ♂♂ are slightly darker, with a greater contrast between the brown femora and paler tibiae. They differ from southern ♂♂ also in having the upper facets of the eyes markedly enlarged, though not sharply separated from the small lower and posterior facets. No differences were found in the genitalia.

The fourth form of the species is represented by 3 ♀♀ from Stradbroke I. collected by E. N. Marks in 1948 and H. A. Standfast in 1955, but not by the type of *angusticallosus* which is a typical *montana*. They are like the northern *doddi* in some respects, but larger (11–11.5 mm) and much darker. They differ from typical *montana* in being more slender; with shorter hairs on eyes; narrower frons (index 3.5–4); rather characteristically shaped antennal plates (Fig. 104 A); more uniformly dark brown bodies, the scutal vittae and apical bands on abdominal tergites being merely a lighter brown than the ground colour; more uniformly

brownish wings; and the white-haired median triangles on the abdominal tergites restricted to the 2nd and 3rd or 2nd to 4th.

The ♀ genitalia also vary considerably; but there was no correlation with external characters, *niger* and *montana* forms both having sternites like those in Figures 116 and 118, a black A.C.T. ♀ agreeing closely with a very pale one from Woodford (Fig. 117), and the form from Stradbroke I. having a similar 8th sternite, but a furca more like that of *doddi* (Fig. 119).

Distribution.—QUEENSLAND: Beatrice R., Oct., biting, M.J.M.; Mt. Spec (Little Crystal Ck.), Nov., M.J.M.; Eungella, Oct., Goldfinch, Turner; Yeppoon, Sept.: Rockhampton (old ♀ ♀ in Macleay Museum, locality doubtful); Maryborough, Oct., Grenie; Woombye, Nov., Beri; Buderim Mt., Dec., C.J.W.; Blackbutt, Dec.; Bunya Mts., Dec., Perkins; Kilcoy, Nov., Dec.; Woodford; Stradbroke I., Dec., Mar., Hacker, Marks, Standfast; Toowoomba, Dec., Greaves; Mt. Tamborine, Davidson, Froggatt, Lea; Binna Burra, Dec., M. & M.; Wilson's Peak, Marks; National Park, 3000 ft, Nov., Dec., Carter, Hacker, I.M.M., Perkins, Tiegs; Lamington, Oct., Perkins. NEW SOUTH WALES: Undercliffe Falls, Jan., Perkins; Barrington Tops (Carey's Peak, Tubrabucca Ck., 3800 ft level), Jan., Mar., McMillan, Pescott and Burns, S.U. Zool. Exp.; Wolgan R., Feb.; Blackheath, Jan.; Jenolan Caves, Wiburd; Sydney (Mosman), Oct., Mar., Goldfinch, Wirth; National Park, Jan., Apr., I.M.M.; Helensburgh, Mar., Ferguson; Mt. Keira, Dec., Chadwick; Shoalhaven R., Dec., McMillan; Tinderry, Jan., I.M.M. AUSTRALIAN CAPITAL TERRITORY: Blundell's Feb., Tonnoir; Bendora, Feb., Mar., Paramonov.

MESOMYIA (MESOMYIA) SULCIFRONS (Ferguson)

* *Silvius sulcifrons* Ferguson, 1921*b*, p. 14; Ferguson and Hill 1922, p. 246 (possibly *Mesomyia*). Type ♀, from Perth, in the Australian Museum, Sydney.

Mesomyia (Mesomyia) sulcifrons (Ferguson). Mackerras 1955*b*, p. 609, fig. 15 *E*.

Material examined.—5 ♂♂, 44 ♀♀.

A robust dark brown to blackish species; immediately recognizable by the linear callus, and strong dorsal tooth on 3rd antennal segment. Length 11–13 mm. *Female* (Figs. 98, 106, 122)

Head.—Eyes with long, dense, brown hairs. Frons slightly diverging, index 3, with rather dark brown tomentum and fairly strong black hairs; callus brownish black, approximately linear but irregularly ridged, full length of frons. Subcallus with grey tomentum, fawn above insertions of antennae, and with strong black hairs on the whole of the grey part; parafacials and face grey, with black hairs laterally on the parafacials, white ones in the facial groove, and shorter black ones on each side of the face. *Antennae*: 1st segment with dark grey tomentum, 2nd dark brown, both with black hairs; 3rd strongly toothed above, with reddish brown plate and dark brown style. Palpi dark greyish fawn; 1st segment with strong white hairs, 2nd with short black hairs. Beard white.

Thorax.—Scutum and scutellum dark brown, with grey dorsocentral vittae which narrow to a point at or behind suture, and grey lateral areas; hairs mixed black and creamy yellow on disc, mainly black in the presutural lateral area, and whitish mixed with black above and behind wing root and in front of scutellum; marginal hairs of scutellum whitish at sides, black towards median line. Pleura grey, with white hairs, except for black ones on upper mesopleural convexity.

Legs.—Coxae similar to pleura. Femora deep brown to black, with black hairs; knees yellowish; fore and mid tibiae bright brown, hind darker brown, the fore pair with dull golden and dark brown hairs, mid and hind with black hairs. Tarsi dark to blackish brown, with black hairs.

Wings.—Brownish grey, darker in costal cell, and sometimes some vague darkening in radial area; stigma scarcely developed, vaguely brown; veins brown; sc setulose below; R_4 usually without appendix.

Abdomen.—Variable. In some specimens, 1st tergite greyish, and the remainder brownish black, with black hairs; 2nd to 4th with narrow yellowish brown apical margins, and conspicuous median apical triangles and sublateral zones of white hairs; 5th and subsequent tergites entirely dark-haired. Venter brownish black, with paler apical margins, and mainly creamy white hairs on 1st to 4th sternites, entirely dark on the others. In other specimens, ground colour of 2nd to 4th tergites bright yellowish brown, with a darker median vitta, and the paler hairs marking the median apical triangles and sublateral areas more yellowish cream; venter also predominantly yellowish brown on the basal 3 or 4 sternites. There are all gradations between the two extremes.

Male (Figs. 17, 27)

Similar to ♀, but, as usual, more hairy. Eyes with very dense strong brown hairs; upper facets not perceptibly enlarged. Hairs on parafacials and face dense, mixed black and dull creamy brown. Tooth on 3rd antennal segment particularly strong. Palpi cylindrical, tapering to a point, with long dense brown to creamy brown hairs. Thorax, legs, and wings as in ♀; but scutum darker, and fore and mid tibiae paler and contrasting more with the femora. The abdomen resembles the pale form of the ♀, and the median darker vitta is particularly well defined.

Distribution.—WESTERN AUSTRALIA: Mundaring, Clark; Darlington, Nov., Calaby; National Park, Nov., Burns, Wilson; Perth (Swan R.), Nov., Hardy, Newman, Nicholson.

MESOMYIA (MESOMYIA) TEPPERI (Ferguson)

* *Silvius tepperi* Ferguson, 1921a, p. 370. Type ♀, from Adelaide, J. G. O. Tepper, in the South Australian Museum, Adelaide.

Mesomyia (Mesomyia) tepperi (Ferguson). Mackerras 1955b, p. 609, figs. 15 B, G.

Material examined.—1 ♀.

A dark brown species, with a superficial resemblance to *Ectenopsis (Parasilvius) victoriensis* Ferg. Hairs on eyes short; frons medium; callus narrow, but distinctly expanded; antennae with basal plate rounded above; palpi short. Length 14 mm. To be distinguished from *latifrons* by the brown rather than greyish colour, somewhat smaller size, and much narrower frons.

Female (Figs. 100, 107)

Head.—Eyes with moderately dense but inconspicuous brown hairs (not bare as described by Ferguson). Frons diverging, index 3, with dark brown tomentum (which may be somewhat greasy) and brown hairs; callus brown, irregularly grooved longitudinally, about half width of frons at base, and narrowing to just

below anterior ocellus. Subcallus, parafacials, and face with fawn-brown tomentum; subcallus apparently without hairs; parafacials and face with dull cream hairs, mixed with some brown ones below antennae. *Antennae*: 1st and 2nd segments dull brown, with dark brown hairs; 3rd brownish black, rather short, with rounded dorsal angle. Palpi brown, with cream hairs on 1st segment, short brown ones on 2nd. Beard creamy white, rather sparse.

Thorax.—Scutum and scutellum dark greyish brown, lighter brown in lateral areas; hairs on disc dark, inconspicuous; marginal hairs mainly dark brown in front of wing root, yellowish cream above and behind it; scutellar hairs dark, with some paler reflections. Pleura brown, with long dull yellowish cream hairs.

Legs.—Uniformly brown, with brown hairs, except for some paler ones on femora.

Wings.—Light brownish grey, darker in costal cell, but without darker markings elsewhere; stigma inconspicuous; veins brown; *sc* bare; *R*₄ without appendix.

Abdomen.—Deep brown, darkening somewhat on more apical tergites, and with narrow paler apical margins, which are somewhat expanded in mid-line on 5th and 6th tergites; hairs dark brown on the darker parts, creamy white on the paler apical margins. Venter dark brown, with brown hairs; apical margins of sternites paler, and with fringes of creamy white hairs. Genitalia not dissected.

Distribution.—SOUTH AUSTRALIA: Adelaide, Tepper.

MESOMYIA (MESOMYIA) LATIFRONS, sp. nov.

Type.—Holotype ♀, from Encounter Bay, S.A., -i.1922, in the School of Public Health and Tropical Medicine, University of Sydney. Although it was found drowned, this specimen is in surprisingly good condition.

Material examined.—1 ♂, 1 ♀.

A large, greyish brown to black species; with wide frons; rather narrow, tapering callus; dark brown legs; somewhat brownish grey wings in ♀; and narrow pale apical bands, which form small median triangles and wider lateral expansions on the abdominal tergites. Length 14 mm (♂), 17 mm (♀).

Female (Figs. 101, 108, 123)

Head.—Eyes with short dense whitish hairs. Frons bulging forward, diverging, index 2, dull greyish fawn, widely grey on eye margins, with short but strong black hairs; callus dark brown, less than one-third width of frons at base, and tapering to a narrow line at anterior ocellus. Subcallus, parafacials, and face greyish white, the face with a fawn tint; hairs white, extending above level of antennae on subcallus, long and mixed with some dark ones on face. *Antennae*: 1st and 2nd segments brown, with black hairs; 3rd missing. Palpi light fawn, 1st segment with long white hairs, 2nd with short brown hairs. Beard well developed, white.

Thorax.—Scutum and scutellum rather dark brown, with narrow grey median line ending before the suture, somewhat wider grey dorsocentral vittae,

which fade behind the suture, and grey lateral areas, with a brown fleck above wing root; hairs on disc white to creamy white, long and relatively dense; marginal hairs dark brown in presutural area, white elsewhere. Pleura with pale grey tomentum, with some brown showing through on upper mesopleural convexity; hairs white to pale cream, long and dense.

Legs.—Brown, somewhat darkened on hind tibiae and tarsi; hairs mixed brown, creamy yellow, and white on femora, dark brown to black elsewhere.

Wings.—Light greyish brown; stigma ill-defined; veins brown; *sc* bare; *R*₁ without appendix.

Abdomen.—First tergite fawn-grey, with white hairs, remainder dark cinnamon brown, with dark brown to black hairs; apices of tergites narrowly banded with pale grey, which is expanded in the mid-line to form small white-haired triangles, and laterally to form crescentic pale lateral margins, which are conspicuous by reason of the long dense white hairs they bear on 2nd to 4th tergites. Venter dark brown, with narrow yellowish grey apical margins; hairs long, dense, white on 1st and 2nd sternites and on apices of the remainder, dark brown on dark parts of 3rd and subsequent sternites.

Male (Figs. 18, 28, 112)

This specimen has not been made the allotype, because it could possibly be the ♂ of *tepperi*, although it seems more likely to be correctly placed here. It is a black insect, which has been relaxed, and may be darker than normal. Eyes with short, dense, greyish brown hairs; upper facets somewhat enlarged over a relatively small central zone. Subcallus fawn-brown, with a few long hairs at lateral corners; parafacials and face grey, with some brownish reflections and long white to creamy yellow hairs. *Antennae* (Fig. 112): basal segments brown, with greyish overlay and not very long black hairs, 1st somewhat swollen; 3rd brownish black, paler at extreme base, with sharp dorsal angle. Palpi very short, conical, brown, with yellowish cream and some black hairs. Scutum black, with dark grey dorsocentral vittae and lateral areas, and long whitish hairs. Legs with femora blackish brown, other segments deep brown. Wings more uniformly greyish than in ♀, costal cell scarcely darkened; vein *sc* bare. Abdomen (somewhat discoloured) black dorsally and ventrally, with narrow pale margins to tergites and sternites, and long white hairs.

Distribution.—SOUTH AUSTRALIA: Mt. Lofty Ra., Jan., T.S.W.; Encounter Bay, Jan.

MESOMYIA (MESOMYIA) CYDISTER (Taylor)

* *Diatomineura cydister* Taylor, 1918, p. 58; Mackerras 1960, p. 148. Type ♂, from King George Sound, W.A., in the Australian Museum, Sydney. Examination of the type, and dissection of the paratype ♂, showed that the species is a *Mesomyia*.

Mesomyia (*Mesomyia*) *cydister* (Taylor). Mackerras 1955*b*, p. 609, figs. 3 *A*, 15 *I*, *M*, *N*.

Material examined.—3 ♂♂, 3 ♀♀.

A hairy, blackish brown, *Dasybasis*-like species; with wide diverging frons; wide callus; narrow antennal plate; and inconspicuous pale median triangles on abdominal tergites. Length 12.5–15 mm.

Female (Figs. 99, 109, 124)

Head.—Eyes with dense greyish white hairs. Frons markedly diverging, index 2, with greyish fawn tomentum and black hairs, which are dense below the ocelli and on the lower part of the callus; callus shining dark brown, irregular, and filling almost the basal half of the frons, with an extension to the anterior ocellus. Subcallus, parafacials, and face with greyish white tomentum; subcallus and lateral parts of parafacials with long brown hairs; medial part of the parafacials and most of face with dense white hairs. The face is markedly hollow, and the whole appearance of the head is exactly as in a typical *Dasybasis*. *Antennae*: 1st segment somewhat swollen, with fawn-grey tomentum and long black hairs; 2nd light brownish yellow, with black hairs; 3rd brownish yellow at base, the remainder brownish black. Palpi light fawn, 2nd segment with short brown and cream hairs. Beard dense, white.

Thorax.—Scutum and scutellum greyish black, with black hairs, and narrow, not very conspicuous, grey dorsocentral vittae and lateral areas; marginal hairs brown on notopleural lobes, white above and behind wing root. Pleura pale grey, with long dense white hairs, mixed with some brown ones on upper mesopleural convexity.

Legs.—Coxae similar to pleura; remaining segments brown, with some whitish hairs posteriorly on mid and hind femora, black ones elsewhere.

Wings.—Greyish; costal cell darkened, a vague darker cloud from fork of *Rs* across apices of basal cells, and an indication of darker markings at fork of *R*₄₊₅ and apex of discal cell. Stigma brown, inconspicuous; veins brown; *sc* bare; *R*₄ without appendix.

Abdomen.—Deep, almost blackish brown, with dark brown hairs, and well-defined, pale greyish, white-haired apical margins to the tergites; 2nd and 3rd with indications of paler median and lateral apical triangles. Venter light greyish brown, with pale grey apical margins to the sternites; hairs white on 1st sternite, blackish basally and whitish apically on the remainder.

Male (Figs. 19, 29, 115)

Darker and more hairy than ♀. Eyes with dense brownish grey hairs; upper facets slightly enlarged in central zone. Subcallus, parafacials, and face grey, with dark brown and dull yellowish cream hairs; the face extremely hollow. Palpi very short, almost hidden in the facial hair, brown, with long blackish hairs. Legs with femora deep brown to black, tibiae brighter brown, darkening apically and on tarsi. Abdomen black, with greyish cream apical margins to the tergites, the pale colour widening laterally, especially at sides of 1st and 2nd tergites; hairs long and dense, black on the darker parts, creamy white on the paler areas. Venter light brown, with greyish cream apices to the sternites; hairs predominantly creamy white, mixed with black on darker parts of 3rd and subsequent sternites.

Distribution.—WESTERN AUSTRALIA: Perth (Crawley, King's Park), Nov., Burns, Fuller, Norris, Riek; King George Sound.

MESOMYIA (MESOMYIA) IMITATOR (Ferguson)

* *Silvius imitator* Ferguson, 1921a, p. 369; Ferguson and Hill 1922, p. 246 (possibly *Mesomyia*). Type ♀, from Bunbury, W.A., -i.1898, W. R. Mack, in the South Australian Museum, Adelaide.

Mesomyia (Mesomyia) imitator (Ferguson). Mackerras 1955b, p. 609, figs. 15 F, K.

Material examined.—3 ♂♂, 19 ♀♀.

A relatively small, striking, black and white, *Dasybasis*-like species; with wide frons and callus; clearly vittate scutum; and conspicuous median pale triangles forming an incomplete vitta on the abdominal tergites. Length 10–11 mm. There is some variation, and darker specimens will be described first.

Female (Figs. 102, 110, 120)

Head.—Eyes with long cream hairs. Frons diverging, index about 2, with grey tomentum and fairly dense black hairs; callus dark brown, full width of frons at base, and with a rather narrow extension ending below anterior ocellus. Subcallus, parafacials, and face greyish cream, with cream hairs, mixed with some brown ones on sides of face. *Antennae*: 1st and 2nd segments dark brown, with greyish tomentum on 1st, and black hairs above, pale ones below; 3rd short and wide, blackish brown, a little paler at extreme base. Palpi fawn-brown, 1st segment with cream hairs, 2nd with brown hairs. Beard cream.

Thorax.—Scutum blackish brown, with wide, conspicuous, grey dorsocentral vittae and lateral areas, which tend to meet anteriorly and at suture, so that the sublateral brown colour is often divided into two oblong bars; hairs brown, except on shoulders and above and behind wing root, where they are greyish white. Scutellum deep brown, with pale grey lateral corners; hairs black on the darker parts, greyish white laterally. Pleura grey, with rather long and dense dull cream hairs.

Legs.—Coxae similar to pleura. Femora blackish, with black hairs on fore pair, mostly dull yellowish cream on mid and hind; tibiae brown, darkening apically and on tarsi, hairs black.

Wings.—Clear, costal cell brown; stigma dark brown, well defined; veins dark brown; sc setulose below; *R*₁ sometimes with short appendix.

Abdomen.—Black; tergites with paler apical margins, conspicuous greyish white median triangles which tend to develop into a vitta on 4th and subsequent tergites, and pale grey lateral margins; hairs black on the darker parts, greyish white on the paler areas. Venter grey, with greyish cream apical margins to the sternites and cream hairs.

Some females are paler; with an almost parallel frons; bright reddish brown callus; greyish white subcallus, parafacials, and face; more reduced scutal ground colour; clearer wings; and the white abdominal vitta more continuous on 4th and subsequent tergites. They agree with the darker form in other respects, and I believe that they represent no more than a variant.

Male (Figs. 20, 30, 114)

Darker and more hairy than ♀. Eyes with long, dense, greyish cream hairs; upper facets somewhat enlarged, not as dark as the small lower and posterior facets. Subcallus strongly pouting, greyish, with long, dense, creamy white hairs; parafacials and face light greyish fawn, with long, dense, creamy white to yellowish cream hairs; the parafacials bulging strongly, and the face recessed. Palpi slender, rod-like, brown, with cream and brown hairs. Scutum blackish brown, with vittae almost completely obscured, and long dark brown and whitish hairs. Legs and wings as in ♀.

Abdomen black, with apical corners of 1st and lateral parts of 2nd and 3rd tergites variably bright to yellowish brown, reducing the ground colour to a broad vitta; apical margins of all tergites narrowly pale, extended into indefinite median triangles; hairs black on most of disc, yellowish cream in a patch on each side of mid-line on 1st tergite, and on apical margins, median triangles, and lateral corners of all tergites. Venter with first 3 sternites bright to yellowish brown, irregularly darkened, remainder dark brown; all with well-defined pale apical bands; hairs mostly cream, with some black ones on discs of some sternites.

Distribution.—WESTERN AUSTRALIA: Coorow, Nov., Common; Marchagee, Oct., Calaby; Watheroo, Oct., Calaby; "Cranmore Park", near Moora, Oct., Fuller; Merriden, Newman; Cannington, Oct., Norris; Bunbury, Nov., Jan., Common, Mack; Collie, Nov., McIntosh and Calaby; Bowelling, Nov., McIntosh and Calaby.

MESOMYIA (MESOMYIA) NIGERRIMA, sp. nov.

Type.—Holotype ♀, from 25 miles W. of Ravensthorpe, W.A., 23.xi.1958, E. F. Riek, in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Material examined.—5 ♀ ♀.

A compact, black species; close to *imitator*, but distinguished by narrower frons, less evident scutal vittae, darker wings, and absence of pale median triangles on the narrowly fasciate abdominal tergites. Length 10–11 mm.

Female (Figs. 103, 111, 121)

Head.—Eyes with short, dense, brown hairs. Frons relatively narrow (index between 2.5 and 3), diverging, with dark grey tomentum and short black hairs; callus full width of frons, except for narrow grey marginal strip, blackish, sometimes more brownish below, irregular above, and with vague median ridge and extension. Subcallus grey, cream on margins, brown around antennae, with short black hairs; parafacials and face grey, with some ashy reflections and light brown ground colour showing on lower part of face; hairs short, black, mixed with some ashy ones. *Antennae*: 1st and 2nd segments with grey tomentum and short black hairs; 3rd black, with wide basal plate and prominent dorsal angle. Palpi distinctly hollow at base, fawn-brown, darkening at tip, with fawn-cream hairs. Beard sparse, white.

Thorax.—Scutum and scutellum blackish brown, rather shining, and with diffuse grey dorsocentral vittae and lateral areas; hairs mixed black and ashy;

notopleural hairs black, supra- and postalar tufts not differentiated. Pleura grey, with dull cream to ashy hairs, and some black ones on upper mesopleural convexity.

Legs.—Blackish brown to black, basal halves of fore and mid tibiae brown; hairs predominantly cream on mid and hind femora, black elsewhere.

Wings.—Greyish brown, darker in costal cell, across apices of basal cells, apex of discal cell, fork of R_{1+5} , and around the deep brown conspicuous stigma; veins dark brown; *sc* setulose below; R_1 angulate, with variable short appendix.

Abdomen.—Tergites rather shining brownish black, with greyish overlay on 1st, and narrow cream apical bands, but no evident median triangles, on 2nd to 5th or 6th, becoming inconspicuous posteriorly. Hairs inconspicuous black and conspicuous ashy white, the latter most evident on disc of 1st tergite and lateral and apical zones of 2nd to 4th. Venter similar to dorsum, but with more evident greyish overlay, and greater distinction between the ashy hairs on basal 4 and black ones on distal 3 sternites. Genitalia with 8th sternite and base of furca narrower than in *imitator*.

Distribution.—WESTERN AUSTRALIA: 1 mile N. of Watheroo, Oct., Calaby; Ravensthorpe, Nov., Riek; Stirling Ra., Nov., Riek.

IX. EXCLUDED SPECIES

The following species are excluded from the Australian Chrysopinae:

Chrysops testaceus Macquart, 1850, p. 38; Froggatt 1911, p. 13; Ricardo 1915c, p. 264; White 1915, p. 17; Surcouf 1921, p. 155; Ferguson 1926a, p. 301; Kröber 1929, p. 520 (*Psilochrysops*). Type ♀, "de la Tasmanie, M. Bigot", in the British Museum (Natural History). The locality is now known to have been erroneous, the species being a synonym of *C. tristis* (Fabricius, 1792), Neotropical (Oldroyd 1947b, p. 277).

* *Silvius minor* Taylor, 1918, p. 62. Type ♂, from "South Australia", in the Australian Museum, Sydney. A *Caenoprosopon*, Pangoniini, from Queensland (Mackerras 1956b, p. 440).

* *Silvius nitescens* Walker, 1857, p. 124. Type ♂, from Australia, in the British Museum (Natural History). A synonym of *Scaptia* (*Scaptia*) *aurata* (Macquart, 1838), Scionini (Mackerras 1960, p. 59).

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EXPLANATION OF PLATE I

Australian Chrysopinae. Photographs by M. J. Mackerras

- Fig. 1.—*Chrysops australis* Ric., ♀.
- Fig. 2.—*Pseudopangonia australis* Ric., ♀.
- Fig. 3.—*Phibalomyia carteri* (Tayl.), type ♂.
- Fig. 4.—*Mesomyia* (*Lilaea*) *fuliginosa* (Tayl.), ♂. Note large *Tabanus*-like head and characteristic abdominal pattern.
- Fig. 5.—*Mesomyia* (*Pseudotabanus*) *frontalis* (Ric.), ♀.
- Fig. 6.—*M. (Ps.) taylori*, nom. nov., ♀.
- Fig. 7.—*M. (Ps.) silvester* (Bergr.), ♀.
- Fig. 8.—*M. (Ps.) alcocki* (Sum.), ♀.
- Figs. 9-12.—Wings of females: 9, *M. (Ps.) nigripennis* (Ric.); 10, *M. (Ps.) fergusonii* (Ric.); 11, *M. (Ps.) fuscipennis* (Ric.); 12, *M. (Ps.) distincta* Ric.

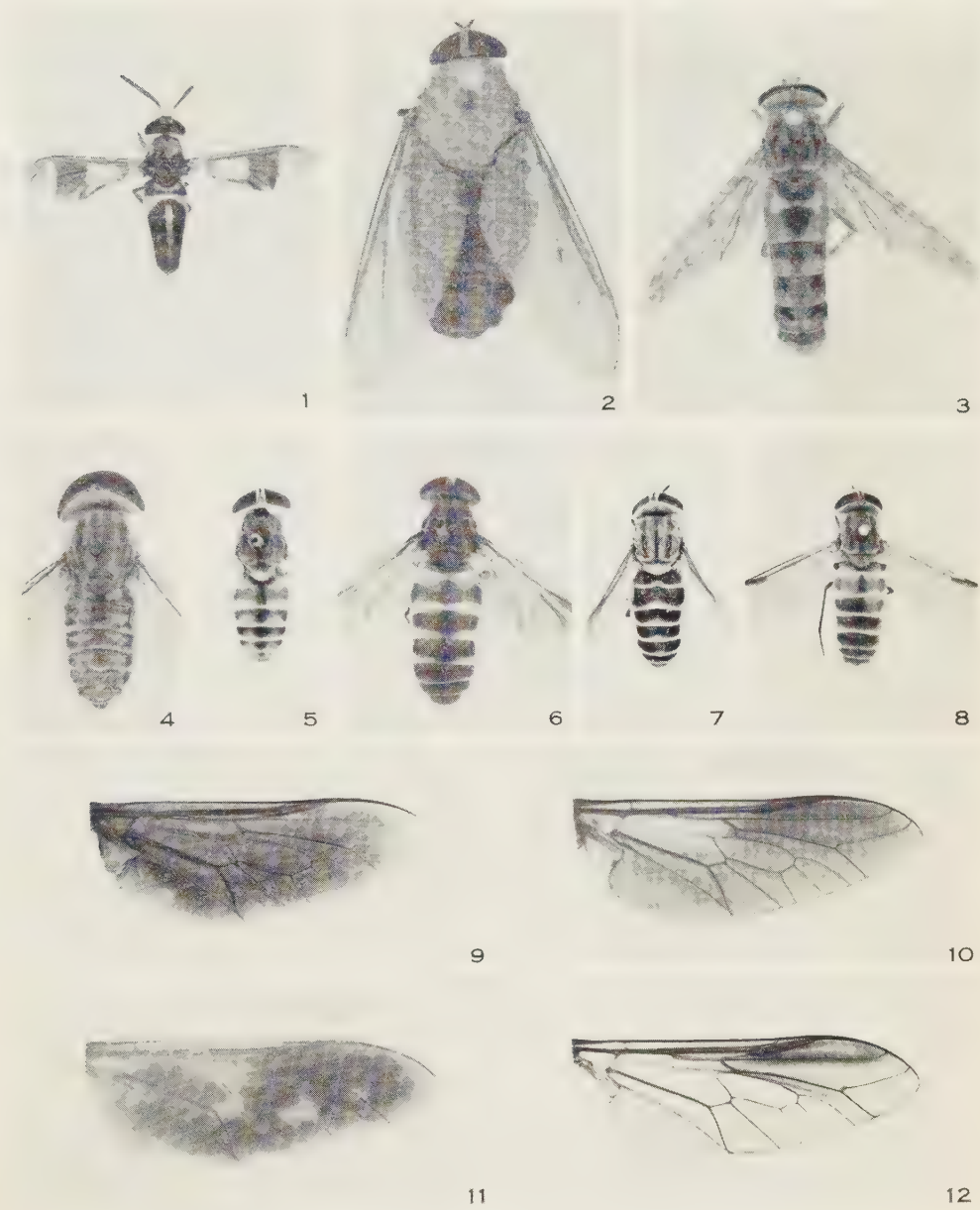
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